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Herbert F. Bergman

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OXYGEN DEFICIENCY AS A CAUSE OF DISEASE IN PLANTS

HERBERT F. BERGMAN

U. S. Department of Agriculture

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INTRODUCTION

Free oxygen is necessary for all plants, with the exception of some of the more simple, primitive ones, for the liberation of energy by which life processes are maintained. When free oxygen is absent for more than brief periods, the health of the plants is impaired, that is, the plants become diseased, and if seriousy enough impaired, soon die. The term "disease" as here used is defined by Stevens and Stevens (1952) as "Any impairment of structure or process of sufficient intensity or duration to noticeably or permanently affect the normal development of the plant. One must include non-pathogenic disorders in this concept".

The significance of deficient soil aeration as a factor in causing disease in plants was realized by a few plant pathologists as early as the latter part of the nineteenth century. Sorauer (1874) appears to have been the first to become aware of it. He mentioned lack of oxygen in heavy soils as a cause of decay of seeds and seedlings, and also called attention to the harmful effects of excess carbon dioxide produced by the decomposition of organic materials in soils with very little or no oxygen. In the second edition of his textbook, Sorauer (1886) pointed out that many plant diseases may be traced to lack of aeration; he discussed silting, compact soils, unsuitable soil structure, too deep planting of trees, and excess water as causes of disease, and cited examples of diseases brought about by the respective conditions.

Hartig (1878) called attention to the slowness or absence of aeration in over-wet soils and applied the term "root-rot" to cases where roots die from lack of oxygen instead of infection by fungi. He described a very destructive root rot in young Scotch pine woods of northern Germany that occurred on poorly drained clayey loam or fine-grained quartz soils. The disease was found also in spruce growing in decidedly shallow soils containing stagnant water.

Relatively few studies on oxygen deficiency in relation to disease of plants were made during the remainder of the nineteenth century. After 1900, largely because of the influence of the second edition of Sorauer's textbook, diseases of plants due to lack of soil aeration received more attention; the importance of adequate soil aeration was pointed out by Mangin (1895), Woods (1901). Graebner (1906, 1909), Metcalf (1907), Selby (1908), Coville (1910) and Hesselman (1910).

The occurrence of many diseases of great economic importance, for which no pathogen could be found, demanded the attention of many

plant pathologists in the United States, Great Britain and other countries during the early part of the twentieth century. The most important among these were diseases of fruits and vegetables, particularly apples and potatoes, which occurred frequently and extensively in the large-scale storage and shipment of these products. The occurrence of other non-pathogenic diseases of several crops of great economic value, as a result of deficient soil aeration, also presented problems requiring attention.

A voluminous literature on plant diseases has appeared since, but relatively few papers have dealt with diseases due to a deficiency of oxygen in the soil. Plant pathologists appear to have had little interest in such problems. A very large part of our knowledge of soil aeration and of the effect of a deficient air supply to plant roots on physiological processes in plants has been obtained in studies by plant physiologists, agronomists, horticulturists, ecologists and physicists. This knowledge has contributed greatly to our understanding of the nature of diseases due to oxygen deficiency and of the conditions which cause them.

A very complete survey of the literature, up to 1920, on soil aeration in relation to plant growth was made by Clements (1921) who cited several examples of diseases caused by lack of aeration of soil. Later reviews on soil aeration in relation to plant growth, although not concerned with possible pathogenic effects of deficient soil aeration, include references to papers that contain data which are very important for the explanation of various pathological effects. Among these may be mentioned: reviews on soil aeration as an ecological factor, by Romell (1922) and Conway (1940); reviews on soil aeration in relation to effects on the physiology of plants, by Miller (1938) and Kramer (1949); and reviews on soil aeration in relation to plant growth from the standpoint of agronomy, by Peterson (1950) and Russell (1952).

No attempt apparently has been made previously to review the literature on diseases occurring under conditions of oxygen deficiency. Such a review is undertaken here with consideration of known or possible effects of oxygen deprivation on physiological processes that might lead to pathological conditions or death of plants or which might favor attack by pathogenic fungi.

Plant diseases caused by oxygen deficiency will be considered under three headings: *a*) diseases caused by a reduction in the oxygen supply to the roots; *b*) diseases caused by a reduction in the oxygen supply to

aerial parts of the plant as a result of flooding; *c*) diseases caused by lack of ventilation during storage or transportation.

DISEASES CAUSED BY REDUCTION IN OXYGEN SUPPLY TO ROOTS

Diseases attributed to an insufficient supply of air to plant roots in very compact soils or as the result of the formation of surface crusts have sometimes been observed. Howard (1918) described a disease of wheat in northern India caused by the formation of a surface crust that was very impermeable to air. The crust was formed as the result of irrigation of fine alluvial soils. Howard stated that "Irrigated wheat is often watered six times and the crop shows all the symptoms of poor soil aeration — excessive liability to rust attacks, slowness in ripening, and shrivelled grain of poor quality. . . . A method of growing the crop on a single irrigation was worked out. . . . The method consists in making use of the preliminary irrigation before sowing and breaking up of rain crusts afterwards. . . . Under the new method the yields are often higher with one irrigation than with six or seven. Harvest is about a month earlier and the wheat ripens more normally and develops the characteristic color of the chaff and straw".

A disease of citrus trees in the region of Dortyal (Turkey) caused by too deep planting or hilling of trees was described by Gassner (1941). The trees for many years had shown severe injury and high mortality. In later stages of the disease the bark at the base of the trunks became necrotic and fungi attacked the bark. These fungi were only wound parasites and had no effect on the propagation of the disease. Application of fungicides was of no benefit. Diseased trees could be cured by uncovering the stem down to the roots.

Chlorosis of grapes growing in a heavy soil in the canton of Zurich (Switzerland) was described by Meier (1943). He concluded that the disease was caused by lack of aeration as a result of too deep planting in the heavy soil which was followed by the death of the roots. Unimproved varieties were much less affected, since they formed roots near the surface. Occurrence of the disease in other districts in previous years was mentioned.

Diseases resulting from oxygen deficiency are caused most often by poor drainage or flooding. Coville (1910) called attention to the adverse effect of poor aeration in poorly drained soils on the growth of

the blueberry (*Vaccinium corymbosum* L.). He stated also that "The continued saturation of the soil with water reduced the root growth and enfeebled the whole plant".

Juritz (1912, 1913) reported chlorosis of peach, apricots and pears, followed by gradual death of the trees. The primary cause of chlorosis and dying of trees appeared to be lack of aeration of the roots as a result of poor drainage, although other factors may have contributed.

A particularly destructive root rot of coniferous seedlings in a nursery was described by Graves (1915). He stated that "The disease caused most havoc during the months of March and April when the soil was still soggy from the winter freeze and rains, and when the roots . . . . stood in the greatest need of oxygen for the commencement of metabolic activities incident to the season's growth. The disease did not occur in another part of the nursery where the soil was loose and porous".

Howard and Howard (1915) reported yellowing of peach trees growing in heavy, close-textured soils as a result of frequent irrigation which filled air spaces in the soil with water, thus depriving the roots of oxygen. The yellowing of the leaves was followed by premature leaf-fall.

A disease of sal (*Shorea robusta*), which made it difficult to establish a vigorous growth of seedlings in the valuable sal forests of India, Bengal and Assam, was described by Hole (1918). Establishment of seedling growth was shown to depend primarily on aeration.

Howard and Howard (1920) found that wilt of indigo (*Indigofera arrecta* Hochst.) occurred on impermeable soils during the monsoon period due to a lack of aeration. Wilt did not occur during the rainy season on porous soils where aeration was adequate. Wilt was not equally severe in all years. In some years, as in 1919, when the monsoon rain was about 12 inches less than the average, wilt was negligible. Wilt during the monsoon was not confined to Java indigo but was common on deep-rooted varieties of patwa (*Hibiscus cannabinum* L.) and san (*Crotalaria juncea* L.). Shallow-rooted varieties of these two species were little affected. Surface-rooted species, such as roselle (*Hibiscus sabdariffa* L.), grew well no matter how wet the monsoon was.

Physiological diseases of rice have been reported from many countries and under various names. These diseases have caused serious losses in many areas. In mild forms of disease plants may recover to some extent and produce a fair crop, but sometimes the disease is severe

enough to cause death of the plants. The literature pertaining to these diseases is very extensive, but a very large proportion of it is in publications of countries in which rice is grown extensively, such as India, Burma, Ceylon, Java and Malaya, from which publications are not generally available.

One of the early, extensive studies of physiological diseases of rice was that of Brizi (1906) who produced symptoms of a root rot of rice known as "Brusone", in experiments, by growing the plants in an oxygen-free nutrient solution. Brizi concluded that the disease is due primarily to a functional disturbance of the root system as a result of a deficiency or absence of free oxygen in the vicinity of absorbing roots. Symptoms of disease first became evident in the roots and later in aerial parts of the plant. Although *Piricularia oryzae* was found sometimes in spots on the leaves, Brizi concluded that the fungus was not the cause of the disease, since plants under favorable conditions of aeration were not infected by it.

Van der Elst (1912) described a rice disease in Java which caused death and rotting of roots to levels near the surface of the ground. The condition was attributed to lack of oxygen supply to the roots as a result of poor drainage during prolonged rains. The compact structure of the soil and the presence of reducing substances were considered to be contributing factors.

A disease of irrigated rice known as "straight head" in southern United States was described by Tisdale and Jenkins (1921). It was especially destructive in Louisiana, Texas and Arkansas which comprise the important rice-growing section of the South. All attempts to find a parasitic organism failed. The disease occurred on somewhat loose soil which when irrigated formed a soft, yielding mud, from which the air was pressed out by the water. Experiments proved conclusively that when the soil was properly aerated, the disease was prevented.

The we-kiki-te disease of rice which causes rotting of seedlings in nurseries was shown by Aiyer (1940) to be due to lack of oxygen in the soil. Growers in the Pegu district (Burma), in which the disease occurred, were in the habit of using low-flying fields for seed beds, since water collected in them during the early rains. Drainage was the only treatment which significantly reduced the disease.

De and Mandal (1957), in a study of physiological diseases of rice, stated that the diseases described in the literature probably have a

common cause, since: "(*a*) the disease affects only lowland rice; (*b*) it is associated with very poor drainage; (*c*) it appears when fields have been unduly long under water prior to planting; (*d*) draining the fields is a common remedial measure". De and Mandal state also that "According to Dastur (1937), 'Pan Sukh' disease in India is due to lack of soil aeration", but with reference to their own studies they say: "The results show that lack of oxygen in the soil is not the cause of a physiological disease of rice plant, and further *that the rice plant is capable of growing in soil in complete absence of any external supply of oxygen*".

The conclusion of De and Mandal (1957) that "lack of oxygen in the soil is not the cause of a physiological disease of (the) rice plant" is subject to serious question, however, since they failed to consider the possibility that an air supply to the roots may have been obtained from aerial parts of the plant, as shown by Van Raalte (1940). Their experimental set-up did not preclude this possibility. They also did not take into account the fact that rice has "a highly functional fermentation system", upon which it depends for its ability to germinate and grow in very low oxygen concentrations as demonstrated by Taylor (1942).

The effects on vegetation of a mud-flow on Mt. Shasta, California, were described by Beardsley and Cannon (1930). They pointed out that pines (*Pinus ponderosa* and *P. lambertiana*) showed early injury and were killed within a few months in the area in which the mud-flow was three or more feet deep. The death of the pines was attributed to deprivation of the roots of oxygen.

Loss of wheat, corn, potatoes, tobacco and various vegetable crops by flooding of fields has been observed frequently. Bratley (1930) reported that strawberry plants and highbush blueberries, probably *Vaccinium virgatum* Ait., were killed by submergence. The number of plants killed increased in proportion to the number of days of submergence.

A reduction in the productivity of cacao on clay soils in Trinidad during the rainy season was reported by Hardy (1943). He found that "during wet periods, anaerobic conditions tend to develop most in clay soil and least in a pervious sandy soil. . . . Since growth and reproduction of the cacao trees proceed mainly in the wet season, the productivity of a particular cacao site may be largely decided by the frequency and length of periods of inadequate aeration".

Loustalot (1945) observed that the root systems of pecan trees in

poorly drained soil were severely damaged, and he attributed the deleterious effects to the depletion of the oxygen supply to the roots. He called attention to the need of good drainage for growing pecans and suggested rainfall and inadequate drainage as possible causes of crop failures in orchards subject to flooding during prolonged rainy periods.

The main pathological problem in the cultivation of peaches and other stone-fruit trees along the Nile in Egypt was considered by Fikry (1947) to be that of disease resulting from a high subsoil water table. The disease caused exudation of gum, drying up of shoots and twigs, shedding of leaves, rotting of roots, and finally death of the trees. The severity of the symptoms depended on the height of the subsoil water. Peach and other stone-fruit trees in low-lying lands were badly affected during and immediately after inundation. Fikry found that land with a water table from one to one and a quarter meters below the soil surface when the Nile flood was at its maximum height was most suitable for cultivation.

Cork spot on fruits of Anjou pears and internal breakdown characteristic of fruit senescence in storage, caused by prolonged submergence, were observed by Kienholz (1946) after the second year of flooding, particularly on trees at the lower soil levels. A few pear trees at the lowest soil levels died the first year.

Extensive collar injury to five-year-old apple trees growing in a heavy soil under wet conditions during the summer was described by Cooley (1948). The injury occurred under conditions that apparently precluded winter injury as a contributing factor and appeared to be caused by poor aeration in the waterlogged soil.

An unusual shedding of young flower buds of cotton during the early part of the flowering period in 1928 in the coastal section of South Carolina as a result of poor aeration of the soil during a period of heavy rains was reported by Albert and Armstrong (1931). The loss of young buds was an important factor in limiting crop yields in many areas of that section.

A behavior similar to that observed by Albert and Armstrong (1931) in cotton was reported by Dean (1933) in *Hibiscus militaris*. Plants in aerated cultures flowered normally, whereas in unsaturated soils all the buds blasted and dropped from the plants.

Abscission, in large numbers, of thick-skinned avocado fruits on trees in soil kept very wet over a prolonged period, because of heavy

rains, was observed by Haas (1936). He concluded that "It is possible that such abscission follows a reduced oxygen content of the soil solution which has injured some of the younger roots".

Chlorosis and dieback in citrus in Arizona, apparently caused by excess irrigation, were noted by Burgess and Pohlman (1928). Thorough aeration of the soil necessary for the growth of citrus trees was obtained by holding the water off until the soil approached the wilting point (5-7 weeks) with the result that the trees soon became green and healthy looking. Application of fertilizers failed to bring about improvement, thus showing that the deterioration of the trees was not due primarily to a lack of organic matter or of available food materials.

The development of surface cork and internal corky tissue which could not be distinguished from that caused by boron deficiency was observed by Heinicke, Boynton and Reuther (1940) in apple fruits. The development of cork was shown to be caused by a deficient oxygen supply to the roots of the apple trees as a result of flooding by excessive irrigation. Development of cork in Anjou pears in poorly drained orchards in Washington was reported by Degman (1946).

DEFICIENT AIR SUPPLY TO ROOTS IN RELATION TO INFECTION BY PATHOGENIC ORGANISMS

Fungi are often found in the roots of plants, particularly of those growing in poorly drained soils. Studies made early in the present century had shown that many root rots apparently were favored by an excess of soil water. It was not known, however, whether excess soil water, by adversely affecting the host, makes it more susceptible to infection by parasitic fungi or whether it merely provides an environment favorable, or even necessary, for growth of the infecting fungus. Need for a study of the relation of environment to the inception and development of disease was evident. Realization of this need led to the study of the relation of environment to the incidence of disease by a number of investigators in the 1920's. Most of these studies, however, were limited to the relation of temperature to infection by fungi. Moisture relations were considered sometimes, but usually without reference to the relation of water content of a soil to its air content. When air content was considered it was generally with reference to the relative proportion of the total pore space of soil occupied by water, or with

reference to soil texture. Apparently it was not realized that wet soils, generally, are characterized by low oxygen content.

One of the early studies of root diseases was that of Hole (1918) with reference to a fungus disease of sal (*Shorea robusta*). Hole stated that "Although the sal root fungus (*Polyporous shoreae*) is widely distributed throughout the sal forests of India, so far as is known at present, it only causes serious damage in those wet forests of Bengal and Assam in which the conditions of soil aeration are known to be particularly unfavorable. Bad soil aeration by producing a diseased and sickly condition in the roots may be a factor of great importance in facilitating the attacks of injurious root fungi of this class."

A disease of considerable economic importance in California and other avocado-growing regions, and one which has been studied very extensively, is root rot of avocado, which causes decline and death, sometimes a sudden collapse, of avocado trees. The cause was for many years uncertain. Various investigators (Tucker, 1929; Wager, 1942; Parker and Rounds, 1944; Zentmeyer and Klotz, 1947 a, b; Crandall, 1948) found it was most prevalent in regions or in seasons of heavy rainfall, particularly in heavy clay soils or poorly drained areas, and emphasized the relation of excessive rainfall and lack of drainage to the occurrence of the disease.

Evidence of the necessity of water for infection of avocado roots by *Phytophthora cinnamomi* was presented by Wager (1940) who was able to infect avocados artificially with the fungus when pots in which the avocados were growing were submerged in water for two to three days. He found also that if plants were not over-watered they could remain in soil infested with *P. cinnamomi* for six months without obvious injury.

Crandall (1948), from observations and experiments on trees growing under conditions of high rainfall and often on poorly drained soils of tropical countries, concluded that "The reported experiments which tend to show that *Phytophthora cinnamomi* is a pathogen only when the tree is subjected to conditions of poor drainage, actually probably only reproduce conditions which often occur in regions where the tree is in its normal environment". He believed "that in this and other tropical and sub-tropical *Phytophthora*-induced root diseases the effect of the change toward wetter environment is more important to the fungus parasite than to the host". Crandall stated also that "chlorosis

and sudden wilting as well as slow decline and dieback either of mature or nursery age trees are two manifestations of the same disease. *Phytophthora cinnamomi* has been isolated from both types of infection. The pathogenicity of the strains isolated has been demonstrated by artificial inoculation on trees growing under normal wet conditions, with symptoms of chlorosis and sudden wilting . . . Uninoculated check trees, growing under identical environmental conditions, have remained healthy".

Curtis and Zentmeyer (1949) found that avocado seedlings grown in culture solutions at various oxygen levels from 7.2 to 0.05 p.p.m. and inoculated with *Phytophthora cinnamomi*, all became infected and died after varying lengths of time, regardless of the oxygen level of the solution. "The fungus attack was most rapid at the highest oxygen level (7.2-6.8 p.p.m.). . . . At low oxygen levels (0.5-0.05 p.p.m), the root tips showed the characteristic symptoms of oxygen deficiency, but indications of fungus injury were slow to appear, although all inoculated seedlings finally died. . . Non-inoculated seedlings were not visibly injured at oxygen levels ranging from 7.2-0.9 p.p.m". On the basis of these results they suggested that there are two types of injury in the field: "(1) Injury from root attack by *P. cinnamomi* under conditions of ample moisture and at any level of oxygen from full aeration down to nearly total lack of oxygen, and (2) injury from nearly total exclusion of oxygen from the soil under severely waterlogged conditions". They stated that "No estimate of the relative importance of the two types of injury to trees in the field is warranted".

Zentmeyer and Bingham (1956), in a study to determine the relation of nitrite formed under conditions of reduced aeration to infection of avocado roots, found no evidence that nitrite predisposes avocado roots to infection by *P. cinnamomi;* root injury caused by nitrite did not increase the rapidity or severity of root attack by the fungus. The fungus was more sensitive to nitrite than was the avocado plant". They state that these results "suggest that injury to roots from toxic materials such as nitrite may not be of general significance in disease development. . . . Earlier work on the relation of reduction in oxygen level to disease development (Curtis and Zentmeyer, 1949) indicated that this factor, also, probably is not important. It appears that, primarily, excess soil moisture provides a medium in which this type of fungus

may produce sporangia and liberate zoospores, and in which the zoospores may swim about, germinate and infect roots".

Root rots of many kinds of plants caused by various species of *Phytophthora*, species of *Fusarium*, and *Phymatotrichum omnivorum* have been reported. In all of these the presence of excess water in the soil, as a result of poor drainage during heavy or prolonged rainfall, has been considered as a primary factor in the occurrence of disease. This at least implies a deficiency in the oxygen supply to the roots, although often not specifically stated or definitely established.

Several studies on the effect of different concentrations of oxygen and of carbon dioxide on the growth of a few pathogenic fungi in cultures have been made in attempts to determine the relation of the concentrations of these gases in soil to infection of host plants by specific pathogens. Neal and Webster (1932) showed that the growth of *Phymatotrichum omnivorum* is inhibited by anaerobic conditions and is notably restricted by concentrations of carbon dioxide greater than 25 per cent. The fungus does not grow in pure nitrogen or pure carbon dioxide, although it is not killed and resumes growth soon after it is returned to aerobic conditions. Inhibition of growth of this fungus by anaerobic conditions was confirmed by Moore (1937) who found that the fungus grew best at a concentration of 21 per cent oxygen when the fungus was in direct contact with air; growth of the mycelium was reduced when submerged. Growth, particularly in liquid media, was reduced at a concentration of 10.5 per cent oxygen. Metabolic activities were clearly associated with the oxygen supply to the mycelium.

Webber and Webber (1947), by double culture of cotton plants and *Phymatotrichum* in liquid culture under controlled conditions, demonstrated that growth of the organism and infection of cotton plants were directly correlated with the available oxygen supply.

The effect of various concentrations of oxygen and carbon dioxide on growth and survival of two species of *Fusarium* under experimental conditions was reported by Hollis (1948) who found that tolerance of low concentrations of oxygen by *F. oxysporum* was greater than by *F. eumartii*. Growth of *F. oxysporum* ceased at an oxygen concentration well below one per cent but the fungus survived, whereas growth of *F. eumartii* ceased at a higher oxygen level and the mold died under anaerobic conditions. Both organisms made good growth over a wide range of carbon dioxide concentrations, although *F. oxysporum* was

less tolerant of high concentrations of this gas than was *F. eumartii.*

Durbin (1955), using data from studies to determine the effect of various concentrations of carbon dioxide on the growth of various fungi, found that the data fitted a straight-line dosage-response curve when plotted logarithmically. The graphs showed that growth of *Ophiobolus graminis*, *Fusarium oxysporum* and *F. solani* f. *eumartii* is inhibited less by any particular carbon dioxide concentration than is the growth of fungi usually confined to the upper soil layers. Durbin stated that: "Their ability to grow at lower soil levels allows them to escape competition with the many microorganisms that exist at or near the soil surface".

Leach (1930) demonstrated that infection of potato tubers by the black-leg organism (*Bacillus atrosepticus* van Hall.) occurs readily in poorly drained fields as a result of exclusion of oxygen, since its exclusion favors infection by preventing development of cork in potato tubers. Prevention of cork development in potato tubers by exclusion of oxygen was shown by Kny (1889), Appel (1903), Olufsen (1903) and others. Leach concluded that the absence of oxygen in poorly drained fields may be more important for development of the disease than the abundance of the pathogen.

Evidence that infection of certain host plants by specific pathogens is greatly restricted or prevented by excess water in the soil has been obtained by a number of investigators. Hemmi and Endo (1929) found that infection of rice by *Piricularia oryzae* was affected greatly by the amount of water in the soil. Infection by the fungus was much restricted by the presence of water on the soil surface, which was assumed to be due, at least partly, to the fact that the development of the fungus was to a great extent prevented by the lack of oxygen. Hemmi and Suzuki (1931) in experiments with rice seedlings, showed that seedlings grown in dry soil were more susceptible to infection by *Helminthosporium oryzae* and *Ophiobolus miyabeanus* than those grown in humid soil.

Other diseases also appear to be affected by oxygen or carbon dioxide concentrations in the soil. Millard (1923) found that partial immunity to scab (*Actinomyces scabies*) is closely associated with restricted oxygen supply. Scab was far less liable to occur in clay soils than in lighter soils. The severity of take-all disease of wheat (*Ophiobolus graminis*) appears to be determined, to a great extent, by the concentration of

carbon dioxide in the soil. Garrett (1936) reported that the growth of the fungus along wheat roots is related to the concentration of carbon dioxide in the root zone. Soil conditions which promote the accumulation of carbon dioxide permit the most rapid growth of the fungus along wheat roots and thus favor the occurrence of the disease in the field.

Evidence obtained by various investigators, under experimental conditions, shows clearly that the growth of certain parasitic fungi is affected very decidedly by oxygen supply or the amount of carbon dioxide in the medium in which the fungus grows, and that growth of other fungi is affected very little by the amount of either of these gases present. In most of the studies of diseases here reviewed, no attention was given to possible adverse affects on the host of a reduced oxygen supply to the roots or of an increased concentration of carbon dioxide in the root zone as a factor in promoting infection of the host by a specific parasitic organism. Although some plant species may not be affected by a deficient oxygen supply to the roots, or by an increased concentration of carbon dioxide around the roots, because of physiological or anatomical adaptation to such conditions, the possibility of adverse effects on the host should always be considered in studies of the effect of oxygen deficiency or excess carbon dioxide on host-parasite relations. Further studies on the effect of oxygen deficiency or excess carbon dioxide in the soil, or in soil water near the roots, on other hosts and parasites are necessary to determine to what extent infection of a particular host by a specific parasite is promoted or inhibited by oxygen deficiency or excess carbon dioxide, and whether the promotion or inhibition of infection is the result of the effect on the host or on the parasite, or both.

DISEASES CAUSED BY LACK OF OXYGEN SUPPLY TO PARTS OTHER THAN ROOTS

Cranberries are subject to disease caused by a deficient supply of oxygen to the vines as a result of the extensive use of flooding in bog management. Partial or complete loss of the crop on some cranberry bogs in Massachusetts occurred frequently before 1920 as a result of flooding the bogs for insect control. For many years it had been the custom to flood bogs in June, just before the flower buds were ready to open, and, if possible, bogs were flooded during cloudy weather.

Bergman (1921) showed that reduction or loss of the crop was the result of injury or death of the flower buds caused by a deficiency of oxygen in the flooding water and that the deficiency was greater on cloudy days than on clear ones. Many bogs could be flooded without injury, but in some instances this was not possible because of the initially lower oxygen content of the water in the reservoir or pond from which the water was taken. The practice has been abandoned by most growers but when used the flooding period is greatly shortened; bogs are flooded in late afternoon or evening, and the water is drawn off again very early the following morning.

Cranberry bogs sometimes are flooded in summer by surface water from surrounding uplands after heavy rains. If drainage is not sufficient to remove the water promptly, it may remain on the bog long enough to kill the berries, particularly when temperatures are high during the time that the bog is flooded. Berries are more easily killed during July and early August, since they are not mature and, therefore, have a higher rate of respiration which is further increased by high temperatures. Franklin (1947) estimated that 15,000 barrels of berries were lost as a result of flooding by an excessive rainfall in August, 1946. (2.61 inches at East Wareham, Mass.). Loss of berries on many bogs in August, 1955, also was large, although no estimate of the number of barrels of berries lost was made.

Another disease of cranberries which for many years caused serious losses to cranberry growers in Wisconsin, Massachusetts and New Jersey was described by Bergman (1943). The disease still causes considerable loss, especially in more severe winters, in the latter two states. The disease is caused by oxygen deficiency in the flooding water and occurs as a result of flooding bogs during the winter ... a protection against winterkilling. The disease occurs in its most severe form when bogs are frozen over with a cover of snow on the ice. In such cases it often causes the loss of all leaves and death of the terminal (fruit) buds with consequent loss of the crop the following season. When defoliation is only partial, a crop of varying size, according to the extent of the injury, usually is obtained. Even with moderate injury the size of the crop is smaller. Adoption of changes in flooding practices suggested by Bergman (1943) has greatly reduced losses to growers in all the areas named.

Diseases resulting from lack of ventilation of fruits and vegetables

in storage and transportation became a serious problem from 1900 to 1920 as a result of large-scale storage and shipment of these products in the years just preceding and during that time. The great economic importance of these diseases led to the initiation of studies by many plant pathologists in various parts of the world, particularly in the United States and Great Britain, to determine the conditions under which they occurred and to find methods of reducing or preventing them.

Among diseases of this kind of sufficient economic importance to demand attention was blackheart of potato. Bartholomew (1913) found that the disease could be produced by holding the tubers at temperatures from 38° to 45° C. for 14 to 48 hours. Later, Bartholomew (1915) showed that blackheart could be produced by subjecting potato tubers to temperatures from 38° to 48° for 15 to 20 hours with free access of air. The disease was prevented by passing a stream of approximately 94 per cent oxygen over the tubers during the period of heating. A stream of approximately 94 per cent carbon dioxide passed over the tubers caused a decided increase in the severity of the injury. Bartholomew attributed the injury to a deficiency of oxygen in the interior of the tubers as a result of the increased rate of respiration, since, at the temperatures used, the supply of oxygen diffusing inward was used up before it reached the interior tissues, thus causing death of the tissues by asphyxiation.

Stewart and Mix (1917) showed that blackheart could be produced readily by sufficiently reducing the oxygen supply to the tubers. They were able to produce typical blackheart by partly or entirely filling containers with tubers, sealing the containers airtight, and storing them at temperatures from 2° to 24° C. for periods ranging from a few to 58 days. Stewart and Mix showed also that the injury was caused by a deficient oxygen supply, not by any accumulation of carbon dioxide.

Mann and Joshi (1920), in India, reported that potato tubers remained sound for more than 12 days when the tubers were heated to 27° to 30° C., but when heated to 36° C. in ordinary air, blackheart occurred in about six days. At 41° to 42° C. injury was very marked in two days. Replacing the air by carbon dioxide or nitrogen, or coating the tubers with collodion or paraffin to exclude air, caused development of blackheart in 6 to 12 days, at 27° to 30° C.

Bennett and Bartholomew (1924) observed that when potato tubers

of certain varieties were enclosed in jars and heated to 20° to 30° C., they were injured more quickly than those of other varieties and showed injury before the supply of free oxygen in the jars had entirely disappeared, whereas tubers of other varieties required a longer period of heating and did not show injury until the oxygen in the jars was entirely exhausted. It was suggested that these differences in behavior might be due to differences in the permeability of the skins to oxygen. They stated that actual injury is to be attributed to processes initiated as a result of anaerobic conditions brought about in the tissues.

Davis (1926) produced blackheart at a temperature of 45° C. in a CO_2-free atmosphere with abundant oxygen present. He found, however, that preceding the incidence of the disease, carbon dioxide accumulated rapidly and oxygen was depleted until there was more than 50 per cent carbon dioxide and less than four per cent oxygen in the gas in the intercellular spaces of the tubers. The change in the composition of the internal atmosphere was the first change detected. Davis concluded that "At the temperatures used blackheart apparently is the result of high respiratory activity and the failure of gas exchange to keep pace with the respiration rate, but the possible effects of temperature and other factors must not be overlooked".

Singh and Mathur (1937) stated that "Our findings. . . . suggest that the disease is probably attributable to a derangement in the respiratory process of the tubers brought about by an increased temperature and an accumulation of carbon dioxide and depletion of oxygen in the air surrounding the tubers".

Nelson (1926) stated that surface pitting of potatoes and other physiological diseases, such as black leaf speck of cabbage, cauliflower, brussels sprouts and other crucifers, red heart of cabbage and head lettuce, occur under conditions of poor aeration often found in storage and in transcontinental shipments in refrigerator cars. He concluded that all these diseases are caused primarily by an inadequate oxygen supply or by temperatures which prevent use of the oxygen present.

Conclusions of later investigators, however, were not in agreement with those of Nelson. Platenius (1942) stated that "Surface pitting is a physiological disorder which occurs in many fruits and vegetables after exposure to temperatures slightly above the freezing point for a period of one week or longer". He did not agree with Nelson (1926) that surface pitting is associated with an abnormal course of respiration

and that the ultimate cause of pitting is the inability of the tissue to obtain or utilize sufficient oxygen for normal respiration when held at low temperatures. Platenius found that "Cucumbers, peppers, and snap beans developed typical symptoms of pitting at 0.5° C. after periods varying from 10 to 20 days, although no unusual behavior in respiration at that temperature was observed. He stated that the data obtained rendered it extremely doubtful that low temperature injury is the result of suboxidation. Penzer and Heinze (1954) also stated that "skin pitting of citrus fruits, cucumbers, summer squash, and several other fruits and vegetables are examples of abnormalities arising from exposure to low temperatures".

Studies of physiological diseases which occur in storage and transportation have been made mainly on apples and pears, and in those fruits the disease studied most extensively is scald. In early attempts to find the cause of scald, studies were made to determine whether a low content of oxygen or an increased content of carbon dioxide in the atmosphere surrounding the fruit might be the cause of the poor condition of the fruit frequently observed after the fruit have been in storage for some time. Brooks, Cooley and Fisher (1919a,b) obtained conclusive evidence that accumulation of carbon dioxide is not the cause of apple scald and concluded that it is due to volatile gaseous substances such as esters or other products formed in metabolism.

The possibility that some end product of respiration, formed under anaerobic conditions which often develop in storage, might be the cause of scald has been considered by many investigators. Thomas (1925) showed that acetaldehyde, in addition to ethyl alcohol, is a product of anaerobic respiration, but he attributed the death of the cells of apple tissues to the ethyl alcohol formed, although stating that "the absence of oxygen and the presence of the more toxic aldehyde probably aggravate the effect of the alcohol". Harley and Fisher (1927), also, found that acetaldehyde was formed in Bartlett pears under anaerobic conditions and concluded that it was the cause of pear scald. Thomas (1929), however, reported that there is no evidence that the formation of ethyl alcohol and acetaldehyde precedes the incidence of scald and breakdown. Later studies by other investigators failed to show that apple scald is caused by the formation either of ethyl alcohol or of acetaldehyde.

Trout (1930) found no evidence that breakdown in pears is the

result of acetaldehyde production and, as a chain of causation, suggested: breakdown → waterlogging of tissues → anaerobic conditions with CO_2 accumulation → aldehyde formation rather than aldehyde formation → toxic action → breakdown and waterlogging.

Thomas (1931), however, after further studies, stated that with concentrations of carbon dioxide between 13-20 per cent, in the presence of oxygen, brown heart developed, and with carbon dioxide above 20 per cent, apples suffered from aldehyde poisoning.

The suggestion made by Brooks, Cooley and Fisher (1919b) that scald is caused by volatile substance formed in the metabolism of apples led to the study by many investigators of the relation of volatile emanations to the occurrence of scald, but up to the present the cause of scald remains unsolved. A very complete account of studies on the relation of volatile emanations to apple scald is to be found in a review by Penzer and Heinze (1954).

FACTORS TO WHICH OCCURRENCE OF DISEASE IS ATTRIBUTED

Plant diseases which occur under conditions of poor aeration are often attributed to oxygen deficiency. Other factors must be considered, however. In addition to the direct effect on the plant of lack of oxygen there is also the effect of the accumulation of carbon dioxide which has been regarded by some investigators as an important or possibly primary factor in causing disease. Indirect effects, such as the effect on the absorption and translocation of mineral nutrients, or of elaborated materials, may be involved also. A reduction in the oxygen supply, or the accumulation of carbon dioxide, or both, may affect the activity of soil microorganisms and thus cause changes in the supply of mineral nutrients. The accumulation of various intermediate metabolic products formed within the plant as the result of incomplete oxidation of sugars in anaerobic respiration, or the presence of reduced ions, or of toxic compounds formed in the soil solution under anaerobic conditions, also have been considered as causes of disease or as factors contributing to its occurrence.

Data from studies of plant diseases induced by lack of aeration provide very little evidence regarding the relative importance of the various factors as causes of disease. The effects of changes in the complex environment of the soil on physiological processes within the roots or

other underground parts, and on other relationships involved, when the air supply to the roots or other underground parts is reduced, make it difficult to determine the relative importance of any single factor as a cause of disease. Similar difficulties are encountered in diseases which occur in the storage and transportation of fruits and vegetables as a result of changes in the respiratory process brought about by a reduction in the oxygen supply, or by the accumulation of carbon dioxide, or both, with the attendant production of organic acids, alcohols, aldehydes or other products of incomplete oxidation in anaerobic respiration.

Data from other sources, however, are of value in attempting to clarify some of these relationships. Physiological studies on the effect of a reduced oxygen supply on various processes necessary for the maintenance of normal activity and growth of roots and of the entire plant, as well as many chemical and biochemical studies of poorly drained or submerged soils, and the effects of such soils on various biological processes have yielded much valuable information. Various physiological and ecological adaptions in plants which enable them to survive and grow under conditions of a deficient oxygen supply in poorly drained or submerged soils are known also. Such studies have contributed greatly to a better understanding not only of the relation of changes in the plant root environment, particularly with reference to aeration, but also of the relation of the conditions to which fruits and vegetables are subjected during storage and transportation to the inception and development of various non-parasitic diseases with which we are here concerned, as well as of the relation of the altered environment to the infection of plants by parasitic fungi. All these relationships must be considered in any attempt to determine the extent to which a reduced air supply to plant roots or other parts, or the extent to which other factors are to be regarded as causes of disease.

EFFECTS OF REDUCED OXYGEN SUPPLY ON PHYSIOLOGICAL PROCESSES

The marked effect of reduced oxygen supply to roots of growing plants on various physiological processes which determine the rate and amount of growth, and of reduced oxygen supply to fruits and vegetables in storage or transportation on processes which determine their length of life and nutritive value has been demonstrated repeatedly. The effects of oxygen supply on growth and productivity are the most obvious and were the first to be studied.

Growth and Productivity

The effect of a reduced oxygen supply to plant roots on growth has been studied very extensively since it was first demonstrated in the latter part of the seventeenth century that oxygen is indispensable for plant growth. Interest in the influence of oxygen supply to roots on plant growth has continued during the present century.

Hesselman (1910) concluded from field studies that the oxygen content of soil water is the deciding factor for the growth of trees. In spruce stands with bog formations, the trees grew well where the ground water was moving and rich in oxygen; in stands with poor growth, the water contained only traces of oxygen.

Free (1917) found that the rate of growth and weight of dry matter produced by buckwheat grown in nutrient solution were not affected by bubbling oxygen, air or nitrogen through the solution. All plants grew to maturity and nearly all set seed. Free stated that "It appears that the degree of aeration of the culture solution is without important influence on the growth of buckwheat under the conditions described". Stiles and Jørgenson (1917) obtained similar results with buckwheat grown for 30 days in a continuously aerated culture solution that was renewed weekly.

Results opposite to those reported by Free (1917) and by Stiles and Jørgenson (1917) were obtained by later investigators in studies on the effect of aeration of culture solutions on the growth of buckwheat. Andrews (1921) stated that seedlings of oats, mustard *(Brassica nigra)*, peas, buckwheat and sunflower grown in nutrient solution with aeration had larger, more extensive root systems, taller, more vigorous stems, and greater dry weight than plants in unaerated solutions.

Allison (1922) also found that the leaf areas and yields of buckwheat grown in aerated nutrient solution cultures were much superior to those of plants grown in unaerated or drip solution cultures. Results obtained with barley were similar to those with buckwheat.

Allison and Shive (1923) showed that the growth of roots and tops of soybeans in sand cultures was greater with aeration than without it, either with or without continuous renewal of the culture solution. Loehwing (1934) also found that sunflowers and soybeans grown in sand and in loam with aeration were taller, heavier, and had larger, more branched root systems than those grown in unaerated sand or loam.

Boynton and Compton (1943) found that even a slight reduction in the oxygen concentration in a nutrient solution in which apple, prune and peach trees were growing, reduced the number and size of roots produced by the trees.

Increased growth of roots, stems and leaves of tomatoes, as a result of aeration of the medium in which the plants were grown, whether soil, sand or nutrient solution, was obtained by Clark and Shive (1932), Arrington and Shive (1936), Arnon and Hoagland (1940), Durell (1941), Gilbert and Shive (1942), Vlamis and Davis (1944) and Erickson (1946).

Allison (1924) found that the relative dry weights of barley plants grown in a heavy clay soil, with a moisture content of 90 per cent, were lower than those obtained with any other treatment. Plants in soil with 60 per cent water content, without aeration, made a somewhat better growth. The constant flow of culture solution through the soil without additional aeration produced dry weight nearly double that of plants in soil at 90 per cent water content. Direct aeration of the soil was the most effective, resulting in a 120 per cent increase in dry weight.

Knight (1924) noted that the increase in dry weight of maize grown in soil through which air was passed was greater than that of plants in unaerated soil. The increase in dry weight of wall-flowers (*Cheiranthus*) and *Chenopodium album* grown in aerated culture solution also was greater than that of plants in unaerated solutions. Maize plants grown in nutrient solution cultures, however, showed no increase in dry weight as a result of aeration in comparison with plants grown in unaerated solution.

The possibility that aeration of some soils, under field conditions, may not be sufficient for optimum growth of certain crops has received very little consideration. Arnon and Hoagland (1940), however, stated that: "We believe that our experiments suggest the possibility that in a well fertilized soil aeration (or associated CO_2 environment) may often limit the growth of certain crops". Shive (1941), also, pointed out that "a nutrient substrate saturated with oxygen at the equilibrium point with atmospheric air is considerably below the optimum requirement for maximum yields of some species. This consideration may be of great practical importance from the standpoint of agricultural production".

A limited amount of experimental data indicates that aeration in some soils actually is inadequate for maximum productivity of some crops.

Bushnell (1935) obtained consistently higher yields of potatoes from plots in which the soil was aerated by means of plain or perforated tile than from adjoining check plots, and higher yields from plots in which the soil was aerated by perforated tile than from those in which plain tile was used. He found that "Roots were distinctly more abundant around the tile than in the main body of the soil. . . . The results suggested that the potato is peculiarly sensitive to soil aeration, and that insufficient aeration may often be a limiting factor in potato yields on silt loams and heavier types of soils.

An experiment by Boicourt and Allen (1941) showed that the total linear growth per plant of hybrid tea roses, var. Signora, budded on cuttings of *Rosa multiflora* var. *japonica*, in soil, and in a soil-peat mixture (one part peat moss to two parts of clay soil by volume), aerated by means of three lines of four-inch tile laid one foot below the soil surface, was nearly double that of plants in the unaerated plot.

Data obtained by Farnsworth and Baver (1940), Hofer (1945), Smith and Cook (1947) and Baver (1949) also indicate that soil conditions often may fail to provide adequate aeration for maximum growth of certain crops.

Absorption of Mineral Nutrients

The ability of roots to absorb mineral nutrients is of vital importance and very directly and effectively influences the development of plants. The effect of the oxygen supply to roots on the absorption of several mineral nutrients has been shown by various investigators. Data have been obtained by determining the amounts of certain mineral nutrients absorbed: (*a*) by entire plants grown in nutrient solution (*b*) by excised roots in nutrient solution; and (*c*) by plants potted in soil. Studies of absorption by plants grown in nutrient solution were made by Arrington and Shive (1936), Arnon (1937), Pepkowitz, Gilbert and Shive (1944), Vlamis and Favis (1944) and Hopkins, Specht and Hendricks (1950). Studies of absorption by excised roots were made by Hoagland and Broyer (1936), Steward, Berry and Broyer (1936), Vlamis and Davis (1944) and Woodford and Gregory (1948). Plants grown in sand or soil cultures were used by Loehwing (1934), Heinicke, Boynton and Reuther (1940), Vlamis and Davis (1944), Lawton (1946), Hammond, Allaway and Loomis (1955) and Patrick and Sturgis (1955).

Hofer (1945), by studies of plants in the field, obtained evidence

that soil aeration in the field may be deficient to an extent that affects fertilizer absorption and growth in corn. Hofer reported that many fields of corn in the midwestern States failed to respond to fertilizer treatments when large amounts of fertilizers were placed in the plow furrows when the fields were plowed. Evidence of suffocation of the roots and starvation were apparent when the roots of unresponsive plants were examined. This condition occurred mostly in heavy-textured soils, either because of poor drainage or because the tilth or porosity of the soils had deteriorated due to depletion of the original organic matter. In some fields the penetration of oxygen was adequate to only three or four inches below the surface, or sometimes to the plow sole, and in such cases the roots of the corn plants remained healthy to that depth.

Water Absorption, Transpiration and Photosynthesis

Absorption of water by plants growing in soil or in nutrient solution has been shown by various investigators to be seriously reduced by a deficient oxygen supply to the roots. Livingston and Free (1917) found that *Coleous blumei* and *Heliotropium peruvianum* growing in soil ceased to absorb water within 12 to 24 hours after the soil atmosphere was replaced by nitrogen. Wilting and death followed within one to six days. Absorption of water by *Salix nigra* was not affected.

Bergman (1920) reported that seedlings of bean (*Phaseolus*) and plants of *Impatiens* and *Pelargonium* potted in soil soon wilted after the roots were submerged. Plants of *Impatiens* began to wilt in two days. In three days they were badly wilted, and in four days were wilted beyond recovery. Plants of *Pelargonium* and *Phaseolus* began to wilt on the fourth or fifth day.

Childs (1941) found that photosynthesis and transpiration of individual healthy leaves of one- and two-year-old McIntosh and Delicious apple trees potted in sandy loam soil did not decrease until the oxygen concentration about the roots was two per cent or less.

Childers and White (1942) observed that when the roots of young apple trees growing in soil were submerged, transpiration and apparent photosynthesis were reduced, usually within two to 7 days, and when submergence was continued, sometimes became so small that they could not be measured. Whitney (1942), also, noted that a deficient supply of oxygen to the roots of potted plants resulted in decreased transpiration and death of tomato, tobacco and coleus.

Caughey (1945) found that, in certain bog species, transpiration was reduced by flooding the soil in July. Six days after the roots were submerged the rate of transpiration in *Ilex* decreased to less than ten per cent, in *Gordonia* to 36 per cent, and in *Clethra* to 60 per cent of the pre-test rate.

Loustalot (1945) observed that the rate of photosynthesis in leaves of pecan seedlings with submerged roots was reduced to 11 per cent of normal five days after submersion, and in leaves of plants in flooded soil it was stopped entirely.

Parker (1950) found that flooding the roots of two-year-old seedlings of white oak, swamp chestnut oak, red oak, red cedar and loblolly pine growing in metal containers caused a similar decrease in the rate of transpiration of all four species. In one experiment the transpiration of dogwood decreased rapidly, and the leaves fell off the third day after flooding. In a second experiment the following year, the leaves did not die until three weeks after the roots were flooded.

Kramer (1951) reported that in experiments with tomato, tobacco and sunflower, transpiration and the capacity of the roots to absorb water was reduced rapidly after flooding. Injury to the shoots was more severe when the pots were sunk in soil than when they were submerged directly in water. Plants potted in soil were injured more than plants potted in sand. Tobacco was injured most by flooding, sunflower least; injury to tomatoes was intermediate. Great differences in the behavior of two species of woody plants were observed: "Transpiration of privet decreased rapidly after flooding, and the plants were practically dead after 12 days, while transpiration of loblolly pine seedlings was still above the control rate and was not seriously decreased until after nearly a month of flooding".

Translocation

No studies apparently have been made on the effect of a reduced supply to or exclusion of oxygen from the roots on translocation, although a few studies on the effect of exclusion of oxygen from stems and other parts have been made. Curtis (1929) showed that when the petioles of bean leaves were enclosed in tubes containing nitrogen under slight pressure, translocation was checked. Curtis also obtained evidence showing that translocation which takes place mainly through the phloem tissues, is dependent on the activity of living cells, and that it seems

highly probable that the movement is dependent on the streaming of the protoplasm in the phloem cells.

Mason and Phillis (1936) observed that the exclusion of oxygen from a portion of the stem of cotton greatly reduced the transport of carbohydrates and of mineral nutrients to the bolls.

duBuy and Olsön (1940) showed that transport of auxin in *Avena* coleoptiles is prevented by an absence of oxygen, since auxin transport is dependent on protoplasmic streaming which requires free oxygen as a source of energy and soon ceases when free oxygen is no longer available.

Respiration

Very few studies concerned entirely with the effect of low concentrations of oxygen on respiration have been made. Many of the studies were made in the development of commercial methods of storage of fruits and vegetables in modified atmospheres in which the oxygen content is lower and the carbon dioxide content higher than in normal air.

Parija (1928) observed that the production of CO_2 by apples was lowest in five per cent oxygen and increased above and below that concentration. Long exposure to nitrogen appeared to have no disturbing effect on respiration.

Choudhury (1939) found that potatoes maintained a relatively constant rate of respiration in oxygen concentrations ranging from 6.2 to 98.6 per cent. The rate of respiration of artichokes was reduced by concentrations of oxygen below that in air; but when the oxygen content was greater than 20 per cent, there was no change. In carrots the rate of respiration increased with every increase in oxygen concentration. In nitrogen the respiratory rate of potatoes, artichokes and red beets was reduced; in carrots the anaerobic rate rose gradually to above the normal and maintained the increased rate for 117 hours.

Platenius (1943) showed that, within the range over which tests were made with five vegetables, any decrease in the concentration of atmospheric oxygen caused a corresponding drop in the rate of oxygen consumption. The relation, however, was not a linear one: "An increment in the oxygen content of the air caused a greater increase in oxygen consumption at low levels of oxygen than it did at levels close to normal". Platenius concluded that oxygen became a limiting factor

of respiration whenever its concentration fell below that of normal air. The critical oxygen concentration below which tissues of vegetables in storage were injured as a result of anaerobic respiration was about one per cent for spinach and snap beans, 2.5 per cent for asparagus, and four per cent for peas and carrots when held for several days at 20° C.

Vlamis and Davis (1943) observed that the oxygen consumption of barley and rice seedlings decreased rapidly as the oxygen concentration in the air in which the seedlings were held was reduced below 9.5 per cent.

Biale (1946) found that the rate of respiration of Fuerte avocados in 10 per cent oxygen was less than 80 per cent of that in air and decreased progressively with further reduction in oxygen concentration. Avocado fruits were very sensitive to anaerobic conditions. When fruits were kept in pure nitrogen, a brief increase in CO_2 production was followed by a sharp decline in the respiratory rate to about five mg. CO_2 per kilogram per hour.

Biale and Young (1947) observed that the rate of CO_2 production by lemons was very noticeably affected by the oxygen concentration. In fruits in 34.1 per cent oxygen, the rate was only slightly above that of fruits in air. In oxygen concentrations below that in air, the rate of CO_2 production at once dropped sharply until a critical oxygen concentration was reached, after which the rate increased. The critical oxygen concentration varied but usually was within the range of 0.5 to 5.0 per cent oxygen.

Leonard (1947) stated that the rate of CO_2 production by green, mature Gros Michel bananas at 68° diminished as the concentration of oxygen was reduced below that in air. The rate in nitrogen containing less than one per cent oxygen was about six mg. per kg. per hour as compared with 14 mg. per kg. per hour in air.

Denny (1948) found that the rate of respiration of potato tubers and in roots of radish, beet and turnip was depressed when the oxygen content of the surrounding air was reduced to about 15 per cent by volume, but the reduced rate was only about five per cent below that of controls receiving 20.9 per cent oxygen. When the oxygen content of the air was reduced from 20.9 to 1.8 per cent, a reduction in the rate of respiration was not established, but there was evidence that this is a marginal concentration below which some reduction in rate may be expected.

Shanks and Laurie (1949) found that the rate of respiration of roots of roses was not reduced to any great extent until the partial pressure of oxygen was reduced to at least two per cent or until the partial pressure of carbon dioxide was increased to above 15 per cent.

Allen and Price (1950) reported that the rate of respiration of the plasmodium of the slime mold *Physarum polycephalum* was not greatly affected by lowering the oxygen concentration to about five per cent, but below that level the rate was reduced, becoming proportional to the oxygen concentration below two per cent. With an oxygen concentration of one per cent the rate of respiration was reduced to 30 per cent of the rate in air. With 0.1 per cent oxygen the rate of respiration was reduced to three per cent of that in air, and in complete absence of oxygen respiration ceased.

Data from these studies, and from others not cited, show that there is great variation in the effect of low concentrations of oxygen on the rate of respiration, depending on the kind of plant or part used. These variations probably are determined by various factors such as the nature of the respiratory system, that is, the kinds of enzymes involved, and possible changes in the respiratory system with age; or they may result from low concentrations of oxygen, and from the kinds and relative proportions of storage materials used in respiration. With reference to the relation of enzymes to the rate of respiration, Platenius (1943) stated that "Little is known about the kinds and quantities of enzymes taking part in the respiration process directly or indirectly. It seems likely that this factor is the most important one of all".

EFFECTS OF CARBON DIOXIDE ON PHYSIOLOGICAL PROCESSES

Experiments to determine the effect of carbon dioxide on physiological processes of plants have been made by many investigators since early in the nineteenth century. Many of these experiments, however, are of limited value because of the conditions used in the experiments. Nevertheless there is considerable evidence that carbon dioxide, at least at certain concentrations, decidedly affects physiological processes of at least some plants. The process on which the effect of carbon dioxide has been studied most often is that of growth.

Growth and Productivity

The amount of carbon dioxide in soil air, or in solution in water, necessary to retard growth varies for different species of plants. Noyes, Trost and Yoder (1914) found that roots of potted plants of Christmas pepper, head lettuce, radishes and string beans were not affected to the same extent by passing carbon dioxide intermittently (8 hours daily) or continuously through the soil at the rate of 650 cc. per hour. Root growth of Christmas peppers was affected more seriously than that of other kinds of plants. Continuous passage of carbon dioxide for three weeks through the soil in which lettuce plants were growing had little effect. The only effect on radishes was a tendency for the roots to grow horizontally. Roots of bean plants, with either intermittent or continuous treatment, penetrated to the bottom of the pots.

Noyes (1914) observed that when carbon dioxide was passed through the soil in which corn and tomato plants were growing, the leaves wilted, drooped and became brownish within a week and were practically brown at the end of two weeks. Tomato plants were more affected than those of corn. At the end of the second week carbon dioxide treatment was stopped and air was readmitted. Tomato plants soon damped off at the base but corn plants began to revive, sent out new growth, and at the end of a week were growing normally.

Free (1917) found that buckwheat growing in nutrient solution wilted within a few hours and died within a few days when carbon dioxide was bubbled through the solution. In one culture in which carbon dioxide was replaced by air after the first day, the plants revived partially but remained permanently smaller than other plants in the experiment.

Hole (1918), in an experiment to determine the effect of carbon dioxide on the roots of sal (*Shorea robusta*) seedlings, found that when the concentration of carbon dioxide in the nutrient solution in which the seedlings were grown reached roughly 500 mg. per liter (25 per cent of saturation) and above, the delicate root-tips and rootlets of vigorous sal seedlings were blackened and killed, and production of new roots was inhibited; and that the appearance of the injured roots resembled that of roots in poorly aerated soil. Although this concentration was greater than that in percolation water from pots in which severely injured plants were growing, Hole believed that the concentra-

tion of carbon dioxide in the soil water near the roots, under field conditions, might be high enough to cause injury. Hole stated further: "It is probable that the injurious action of CO_2 depends largely on the quantity of oxygen available. . . . and that we may define a badly aerated soil as one in which there is a deficiency of oxygen and an excess of CO_2".

Knight (1924) found that maize plants potted in soil through which five, ten and 15 per cent carbon dioxide, respectively, was passed continuously for five days, showed no ill effects at the end of that period. A stream of pure carbon dioxide passed through the soil caused wilting in less than two days. The percentage of carbon dioxide in the soil atmosphere at different time during treatment varied from 53 to 65, showing that relatively high concentrations of carbon dioxide are necessary to kill maize.

Cannon (1925) stated that when the amount of carbon dioxide in the air passed through the soil did not exceed 21 per cent, growth of roots of sweet oranges (Valencia, Ruby) continued when less than two per cent of oxygen was present. Growth went on slowly even when a mixture of 75 per cent carbon dioxide and 25 per cent oxygen was passed through the soil for 96 hours, thus indicating a high degree of tolerance of a large excess of CO_2. Roots of willow (*Salix lasiolepis*) in soil through which air containing 45 per cent carbon dioxide was passed continuously for four days, and in another test in which air containing 50 per cent each of carbon dioxide and oxygen was passed for 72 hours, made growth nearly if not quite equal to that in normal air.

Girton (1927) found that elongation of roots of sour orange seedlings, in sand cultures at 25° C., was suppressed by concentrations of 37-55 per cent carbon dioxide, even with an oxygen content of 17-20 per cent in the soil.

Arrington and Shive (1936) observed that the accumulation of carbon dioxide in culture solutions appeared to have no effect on growth, rate of nitrogen absorption or oxygen content of the solutions.

Childs (1941) stated that concentrations of carbon dioxide in the soil atmosphere, within the limits found, had no effect on the growth of apple trees or on photosynthesis and transpiration. Any depressing effect of high CO_2 concentrations was so slight as to be negligible when compared with the effect of low oxygen concentrations.

Vlamis and Davis (1944) found that carbon dioxide passed continu-

ously through nutrient solution in which plants of rice, barley and tomatoes were growing caused immediate wilting and cessation of growth of all plants. Other experiments with barley indicated that a 20 to 30 per cent partial pressure of carbon dioxide was toxic, even when the entire residual pressure consisted of oxygen.

Leonard (1945) stated that the growth of cotton roots was not adversely affected by CO_2 at a concentration of 15 per cent in the soil and not seriously affected by a concentration of 30 per cent. He stated that concentrations of CO_2 as high as 12 per cent in the soil are rarely found but that it is possible that local accumulations around the roots might be sufficiently high to affect root growth.

Leonard and Pinckard (1946) observed that the growth of cotton roots in nutrient solution was somewhat reduced when air containing 30 per cent CO_2 with 21 per cent oxygen and the remainder nitrogen was passed through the solution, but top growth was not affected. When the concentration was increased to 45 per cent with oxygen remaining at 21 per cent, root growth was greatly reduced and top growth also was reduced. With 60 per cent CO_2 and 21 per cent oxygen there was no root growth, and top growth was greatly reduced, but lateral roots developed when the plants were transferred to solutions through which air containing 21 per cent oxygen was passed.

Shanks and Laurie (1949) found that rose plants with their roots in gravel grew equally well with concentrations of carbon dioxide from 0 to 20 per cent and with concentrations of oxygen from one to 20 per cent.

Absorption of Mineral Nutrients

No studies on the effect of carbon dioxide in soil, and very few on its effect in nutrient solutions on absorption of mineral nutrients, have been made. Vlamis and Davis (1944) found that absorption of potassium by rice plants growing in solution cultures was not noticeably affected by passing carbon dioxide through the solution, whereas its absorption by barley and tomato plants was reduced very greatly.

Chang and Loomis (1945) showed that the absorption of five mineral elements by roots of maize, wheat and rice growing in nutrient solution was significantly reduced by bubbling CO_2 through the solutions for ten minutes out of each hour for 36 hours. Absorption of potassium was reduced most; that of phosphorous and nitrogen was

intermediate between that of potassium and that of calcium and magnesium.

Water Absorption and Transpiration

Data on the effect of carbon dioxide on water absorption and transpiration are limited to those obtained from very few experiments. Caughey (1945) kept the soil of potted plants of *Ilex*, *Myrica*, *Clethra* and white oak saturated with carbon dioxide for five days to determine the effect of transpiration. She stated that "Transpiration rates were reduced in all species by the end of the first 24 hours of treatment. *Ilex* and *Clethra* were the least affected during the five-day period. Transpiration reduced was about 50 per cent in *Clethra*, 55 per cent in *Ilex*, 60 per cent in Myrica, and 70 per cent in white oak. On the fifth day after the treatment was discontinued, *Clethra* and *Ilex* had recovered to approximately 80 per cent of their normal rates, while *Myrica* had recovered to about 50 and white oak to about 35 per cent of their normal rates. Two of the three individuals of white oak died within a week after the experiment was discontinued, but none of the pocosin species was visibly injured by the severe carbon dioxide treatment".

Chang and Loomis (1945) showed that absorption of water by roots of maize, wheat and rice plants growing in nutrient solutions was reduced 14 to 50 per cent by bubbling CO_2 through the solutions for ten minutes out of each hour for 36 hours.

Hagan (1950) found that the rate of water absorption by roots of tomato plants after replacement of the soil air by carbon dioxide was reduced to a greater extent, compared with that of aerated check plants, as shown by relative time of recovery of turgor, than when the soil air was replaced by nitrogen. Hagan concluded that "carbon dioxide has a direct effect on the plant, in addition to that caused by the removal of oxygen". However, the value of Hagan's conclusion is limited somewhat for the reason that the results obtained represent the effect of exclusion of oxygen, upon which is imposed that of carbon dioxide, instead of the effect of high concentrations of carbon dioxide in the presence of sufficient oxygen to satisfy the minimum respiratory requirement of the plant. This is a fault of many experiments to determine the effect of carbon dioxide on physiological processes. The results obtained probably would have been quite different if carbon dioxide with 21 per cent

oxygen had been used to replace the soil air instead of pure carbon dioxide.

Respiration

Most of the studies of respiration in plants have been concerned primarily with the effect of reduction of the oxygen supply, particularly in relation to temperature. A few studies, however, were concerned entirely with the effect of the accumulation of carbon dioxide on respiration.

Overholser, Hardy and Locklin (1931), in a study of respiration in strawberries, found that small increases in the carbon dioxide concentration in the respiration chambers had no depressing effect on the rate of respiration but that there was, instead, a slight increase in the rate with higher carbon dioxide content.

Thornton (1933) determined the rate of respiration of the vegetative parts of several kinds of plants, and of a few fruits, at 25° C. in various concentrations of carbon dioxide with 20 per cent oxygen. The rate of oxygen consumption varied according to the part used. Some showed increases, some decreases, and in others no effect was observed. The increases in oxygen consumption for potato tubers was 100-200 per cent; for onion bulbs, 20-100 per cent; for tulip bulbs, 15-35 per cent; and for beet roots, 60 per cent. Asparagus shoots, lima beans, bananas and strawberries showed decreases of as much as 35 per cent. Varying the carbon dioxide content from 8 to 72 per cent did not affect significantly the rate of oxygen consumption by carrot roots. The length of time that the parts were left in the gas mixtures was important; for periods of less than 20 hours oxygen consumption showed decreases, not increases.

EFFECTS OF PRODUCTS FORMED IN ANAEROBIC RESPIRATION

The frequently observed injury to plant roots or other parts, and sometimes the death of plants, as a result of partial or complete exclusion of oxygen has led to the assumption by many investigators that these effects are due to accumulation of alcohol, acetaldehyde, or lactic or other organic acids produced in the plant under anaerobic conditions. The effect of the accumulation of alcohol and acetaldehyde in apples and pears under anaerobic conditions in storage, and the formation of volatile substances in the metabolism of fruit, particularly that of apples, in

storage, as possible causes of breakdown of tissues of the fruits has been considered previously. Paech (1935), in an attempt to find the cause of death of plants as a result of anaerobiosis, studied the effect of organic acids and actetaldehyde and concluded that death of plants or plant tissues could not be attributed to these substances. Conclusive evidence that the presence of alcohol, acetaldehyde or organic acids of any kind, formed under anaerobic conditions, are ever sufficient in amount to be considered as the cause of injury or death of plants or plant tissues has not been obtained.

EFFECTS OF DEFICIENT OXYGEN SUPPLY IN SOIL ON CHEMICAL AND BIOCHEMICAL PROCESSES

Saturated or flooded soils are characterized by low content or absence of oxygen. This adversely affects chemical and biochemical processes which occur in well aerated soils, and thus may result in the formation of compounds not normally present in soils, at least to an appreciable extent, and may make unavailable some mineral nutrients necessary for normal plant growth. Among compounds produced under such conditions are nitrites, sulfides, particularly hydrogen sulfide, ferrous iron and marsh gas (methane). Injury under anaerobic conditions is sometimes attributed to one or more of these substances.

Among those mentioned, the effect of nitrite on plant growth has been studied more extensively than that of other substances. Most of the studies of the effect of nitrite on plant growth have been made with plants grown in nutrient solutions. Mevius and Dikussar (1930) showed that the concentration of nitrite that can be tolerated by sweet corn seedlings depends upon the pH of the nutrient solution. Growth was normal at pH 4.0 in the presence of one mg. of sodium nitrite per liter, but wilting and injury occurred with two mgs.; at pH 5.0, the seedlings withstood ten mgs. without injury, but not 20 mgs.; at pH 6.4, they withstood 100 mgs., but not 200 mgs.; at pH 7.0, there was no injury with 200 mgs.

Curtis (1949) reported that "seedlings withstood increasingly higher nitrite concentrations at higher pH levels. For example, 5 ppm NO_2 nitrogen caused injury to avocado and citrus root tips at pH 5.0 but not at pH 5.5; 10 ppm caused injury at pH 5.5 but not at pH 6.0; 20 ppm caused injury at pH 6.0 but not at pH 7.0. Avocado seedlings were

more severely injured than citrus seedlings and showed less ability to recover from injury with the production of new roots after treatment".

Bitcover and Wander (1950), in a study of nitrogen absorption by citrus trees, observed that trees of Valencia orange growing in coarse gravel (¼ to inch) wilted "during the warmest period of the year when the source of nitrogen in the nutrient solution was in the form of urea. Concomitant with this wilting was a very apparent accumulation of nitrite in the solutions. Experiments demonstrated that relatively high temperatures were a factor in nitrite accumulation, which could be counteracted by sufficient aeration of the nutrient solution".

There is no evidence that injury from nitrite ever occurs in cultivated soils except under conditions of oxygen deficiency. Moreover, injury by nitrite and that caused by oxygen deficiency are sometimes very difficult or impossible to distinguish. For these reasons it cannot be claimed that an observed injury is due to nitrite, even when nitrites are known to be present in the soil, unless it can be established definitely that the plant in which the injury occurs is not injured by a very low content or absence of oxygen in the soil.

Some investigators believe that the large amount of ferrous iron and sulfides in aquatic muds rich in organic matter are toxic to plants growing on them. With reference to this, Misra (1938) states that "Such may be the case in small ponds under extremely stagnant conditions but the data presented do not show it to be so in English lakes. The presence of large amount of marsh gas and presumably some H_2S may also possibly be injurious to plant growth in localities with peaty mud although it has not proved possible to obtain definite evidence of this".

Allgeier, Peterson, Juday and Birge (1932) found that about 65 to 85 per cent of the gas produced during anaerobic decomposition of bottom deposits from Lake Mendota was marsh gas. The presence of marsh gas (methane) in abundance in the soil of rice fields was reported by Leather (1915).

Vlamis and Davis (1944), in an experiment with barley, rice and tomato growing in nutrient solution, through which commercial methane gas passed, found that "Methane gas caused an absolute cessation of tomato growth immediately on exposure. Barley was reduced by about 60 per cent, a greater loss than in the presence of nitrogen. The methane treatment resulted in a fresh weight increase of rice roots amounting to about 70 per cent over the control".

Sturgis (1936), with reference to soils of rice fields, stated that "The results of previous work and an analysis of data in the literature show that the decomposition of organic matter in waterlogged soils causes the accumulation of reduced products. The actual amounts of the reduced products that are likely to be toxic to irrigated rice have not been determined. . . . Data in the literature indicate that nitrogen may be lost from flooded soils and that the low availability of nitrogen to irrigated rice is a most serious difficulty . . .". Sturgis stated also that a review of the results from fertilizers on rice indicates that "the continuous culture of irrigated rice on soils low in organic matter or through which water drains slowly causes the development of toxic or inhibitory conditions which lower the yield of rice. Under the conditions of poor aeration the lowered oxygen supply in the soil and the accumulation of reduced substances slow up the decomposition processes of bacteria which liberate nitrogen from soil organic matter and cause the soluble phosphates to be changed to less available form".

FACTORS AFFECTING AIR SUPPLY TO ROOTS

Adequate aeration of soil requires sufficient air capacity and relative ease of renewal of the soil air from the atmosphere at all times, especially during periods of active growth. The importance of soil structure, particularly with reference to aggregation and porosity, in determining water and air relationships within the root zone of plants was pointed out by Baver (1949). Swanson and Jacobson (1950), also, stated that "structure has more influence on productivity of the soil than formerly was believed" and that "Cultivation improved soil tilth. . . . This improved soil tilth may have been just as important a factor in plant growth as was soil moisture".

FACTORS AFFECTING AIR CAPACITY OF SOILS

Most soils have sufficient air capacity and porosity to insure adequate aeration. The actual pore space occupied by air in arable soils, according to Russell and Appleyard (1915), is commonly not more than ten to 20 per cent of the volume of the soil. Stephenson and Schuster (1937) concluded that aeration is good in soils with ten to 20 per cent of air space by volume and found that in the soils studied aeration was good to a depth of ten or more feet, whereas in soils with poor aeration the volume of air space was five to ten per cent of the total volume of

the soil. Kopecky (1927) stated that "The most appropriate air capacity for grass ranges from 5-10 per cent, for wheat and oats from 10-15 per cent, and for barley and sugar beets from 15-20 per cent of the soil volume".

The most effective pore space for the maintenance of an adequate supply of oxygen to plant roots is the non-capillary. This varies greatly in soils of different types and particle size. Dojarenko (1926) pointed out that the ratio of non-capillary to capillary pore space undergoes a very abrupt change in value as the average particle size increases beyond one half mm. Most finely divided soils (one half mm.), which include those made up of powdery or colloidal particles, have almost entirely only capillary pores (capillary pore space, 44.8%; non-capillary, 2.7%; total pore space volume, 47.5%). As the soil becomes coarser the pore space volume increases gradually; the general character, however, is completely changed. In going over to soils with particles greater than one half mm. diameter, the non-capillary pore space volume increases abruptly to about half the total pore space volume. Even soils made up of relatively fine particles, in the absence of non-aggregated particles which might occupy the larger pore spaces, thereby making them capillary, may have a favorable proportion of non-capillary to capillary pore space and have a suitable structure.

Boynton (1938), in a study of apple orchard soils, found that a highly productive sandy loam soil, uniform in texture to below the six-foot depth, had a non-capillary pore space of 16 per cent by volume; a uniform silty clay loam of above average producing capacity had between eight and six per cent non-capillary pore space; and a heavy silt-clay soil in which apple trees were short-lived had a non-capillary pore space of five per cent to a depth of four feet, and of only one per cent below that depth.

Fine-grained soils may have a greater proportion of air space than other soils with larger particles and yet be poorly aerated. King (1898) showed that heavy clay soils with a porosity up to 50 per cent of the total soil volume were very poorly aerated as compared to sandy soil with much less air space. The reason is that, although the percentage of pore space is larger, the average diameter of the particles and, therefore, also the average diameter of the pores is very small which greatly reduces the rate of diffusion of air through them.

Bradfield and Jamison (1938) pointed out that soils composed

largely of fine silt are some of the most difficult to manage from the physical standpoint, since the grains are so small that they become closely packed by beating rains or mechanical pressure, thus are made exceedingly hard and intractable and very slowly permeable to both air and water. They stated also that in some cases compound particles formed by the flocculation of colloidal clay may contain thousands of primary colloidal particles, although their size may be measured in microns. Compound particles of this size fit together so closely that the soil becomes practically impervious to both air and water.

Soil Compaction and Surface Crusts

Baver and Farnsworth (1940) pointed out that the amount of pore space may be greatly reduced by compaction, even in soils with a structure that normally provides good aeration. When compaction occurs the greater part of the decrease in porosity results from elimination of the larger pores. They concluded that a non-capillary porosity greater than seven per cent by volume in soils is necessary for the production of good yields of beets with high sugar content and that aeration of the soil is likely to become a limiting factor in growth if the air capacity of the soil is below nine per cent.

Hofer (1945) reported that compaction of the soil greatly reduced sugar beet yields. There was strong evidence that effective air capacity is an important factor in sugar beet production. The detrimental effects of compaction of the soil were greatly increased by excess water.

Baver (1949) stated that as a result of poor aeration in the heavy clay soils of northwestern Ohio, plant diseases, particularly root rots of sugar beets, were increasing in severity and, in many instances, were killing about 50 per cent of the stands. When the air capacity of the soil was increased by a different system of soil management, one of the main effects was reduction in the amount of black rot to less than ten per cent.

Cook (1950), also, called attention to the detrimental effect of soil compaction resulting from general use of tractors and other heavy machinery.

The formation of surface crusts in soils composed largely of fine silt as a result of irrigation was pointed out by Howard (1918); as a result of beating rains, by Bradfield and Jamison (1938). Swanson and

Jacobson (1950) called attention to the importance of breaking up soil crusts to provide better aeration of soil.

Excess Water

The amount of air in soils varies inversely with the water content of the soil and reaches a minimum in poorly drained or flooded soils. Baver (1933) concluded that a soil with 5.9 per cent of air space at a depth of 16 to 30 inches was well drained but that one with an air capacity of two per cent at the same depth was rather poorly drained. Boynton (1938) found that "The soil volume not occupied by water may increase from 1 per cent in early spring to 15 per cent in late summer".

Vine, Thompson and Hardy (1942) showed that some of the deeper layers in certain types of soils of cacao plantings in Trinidad, because of variation in annual rainfall, were probably completely devoid of air during a five-week period of the rainy season and that this condition probably existed for several weeks before, and particularly, after the period in which measurements were made.

Furr and Aldrich (1943) also found that "The percentage of O_2 in the top 30 inches of soil varied widely with changes in soil water tension".

The air content of a soil with the pore spaces filled with water is limited to that in solution in the soil water and to that trapped in small pockets in the soil. The amount of the former is very small, not only because of the often limited pore space in the soil but also because of the low solubility of oxygen in water. Russell and Appleyard (1915) showed that the air dissolved in water-logged soils consists chiefly of CO_2 and nitrogen, and contains practically no oxygen. The supply of oxygen to the roots of plants, as well as the removal of carbon dioxide produced by their respiration and by that of microorganisms in the soil, then depend entirely upon the rate of diffusion of the respective gases through water.

COMPOSITION OF SOIL AIR

The composition of air in soils on which agricultural crops are grown was shown by Russell and Appleyard (1915), Leather (1915) and others to be usually near that of the air above the soil and to vary in its oxygen and carbon dioxide content but little more than three per cent

throughout the growing season. The oxygen content usually decreases and the carbon dioxide content increases with the depth of the soil, as was shown by Boynton and Reuther (1939), Boynton (1941), Boynton and Compton (1944) and others. The oxygen and carbon dioxide contents also vary in different types of soils with the kind of plants growing on them, the extent of cultivation, with seasonal changes, with temperature, water content, with the amount and form of nitrogen, the amount of organic matter in the soil, and the abundance of microorganisms. However, such variations in the composition of soil air usually have no significant effect on plant growth.

Concentrations of oxygen and carbon dioxide in soil, usually near their respective concentrations in the atmosphere, are maintained by diffusion. The importance of diffusion in the aeration of soil was emphasized by Buckingham (1904), Leather (1915), Romell (1923), Penman (1940), Baver (1940), Blake and Page (1948), and Taylor (1950). Studies by Penman (1940), Blake and Page (1948), Taylor (1950) and Van Bavel (1952) showed that within the normal range of porosity found in the soils studied, the rate of diffusion of gases varied directly with the porosity of the soil. Van Bavel (1952) stated that "The values obtained by Penman can perhaps be taken as the most dependable", and concluded that the ratio of the diffusivity of gases and vapors through sand and soil mixtures, ranging in porosity from 10 to 60 per cent of the total soil volume, to that in the gaseous phase has a numerical value of about 0.6, a value near that of 0.66 found by Penman (1940). Studies by Blake and Page (1948), however, indicated that "Different field soils may show different relationships between diffusion rates and porosity", and that "diffusion rates may be very low in soils below about 10 to 12 per cent porosity". King (1908) and Bradfield and Jamison (1935) also pointed out that the rate of diffusion of air through fine-grained soils such as clay and fine silt is very slow or, in some instances, negligible.

De Vries (1950) concluded that "The value of regression lines, based on experiments showing a wide scatter, as given by Blake and Page (1948), seems doubtful", and that "In many cases Penman's value $a = 0.66s$ will represent a reasonable estimate, although it may be somewhat low in soils with aggregated particles".

VARIATION IN ABILITY OF PLANTS TO WITHSTAND REDUCED OXYGEN SUPPLY

Plants of different species differ widely in ability to withstand a reduced oxygen supply to their roots. Livingston and Free (1917) found that *Coleus blumei* and *Heliotropium peruvianum* were exceptionally sensitive to deficiency of oxygen in the soil and showed injury within 12 to 24 hours after the supply became deficient. In contrast, *Nerium* was quite resistant to oxygen deficiency and first showed injury after 26 days in an atmosphere of pure nitrogen. *Salix nigra* also was able to endure complete or almost complete exclusion of oxygen from its roots. Other plants also have been found to be quite sensitive to a deficiency of oxygen in the soil. Bergman (1920) observed that when the roots of plants of *Impatiens* potted in soil were submerged, the plants were badly wilted in three days, and in four days were wilted beyond recovery.

Cunningham (1920) stated that stone-fruit trees died after a week of flooding. Apricots were the most susceptible, next nectarine, then peach. Apples, pears and cherries appeared to be but little affected.

Childers and White (1942) noted that all visible roots of apple trees potted in soil with roots submerged were dead after 18 days. Kienholz (1946) found that apricot trees died within two weeks after being flooded and that a few Anjou pears died during the first year.

Some ornamental plants appear to be moderately sensitive to a deficiency of oxygen. Kramer (1951) stated that plants of privet were practically dead after 12 days of flooding. McSwiney (1949) found that among ornamental plants, *Hibiscus*, *Poinsettia*, *Acalypha* and *Peperomia* were killed by three weeks or less of flooding but that some tropical trees, namely, guava, mango and some species of *Eugenia*, were outstanding in flood resistance.

Grasses also appear to be very resistant to flooding. Bolton and McKenzie (1946) found that timothy and *Phalaris* were not severely injured by flooding for seven weeks under 12-18 inches of water. Porterfield (1945) noted that buffalo grass (*Buchloë dactyloides*) survived after submergence for as long as 19 months under as much as 59 inches of water. Stover, Thornton and Dunlap (1953) reported that Bermuda grass (*Cynodon dactylon*) and nut-grass (*Cyperus rotundus*) survived after at least six months of submergence under six inches of

soil and four feet of water, and showed a light green color within 48 hours after the water was drawn off.

Trees have been found to be very resistant to flooding. Green (1947) stated that "No species (of forest trees) survived 4 years of constant flooding. However, even when trees were permanently flooded, impoundment had little effect the first year. The second summer there was some indication of die-off, with river birch (*Betula nigra*) and silver maple (*Acer saccharinum*) the first to show loss of vigor". Yeager (1949) also observed that "Rate of dying showed wide variation by species, pin oak was the most susceptible to injury by flooding, all individuals of this species dying before or during the third year."

Fruits and vegetables in storage or transportation also vary in tolerance of a reduced oxygen supply. Platenius (1943) showed that "Oxygen concentrations of less than one per cent were sufficient to maintain normal aerobic respiration in spinach and snap beans while shelled peas did not tolerate levels below four per cent. Also, there was evidence that the tolerance to low oxygen increases with the aging of the tissues or with a lowering of the storage temperature".

MEANS BY WHICH PLANTS ARE ABLE TO WITHSTAND REDUCED OXYGEN SUPPLY TO ROOTS OR OTHER PARTS

The ability of plants to survive or grow when the oxygen supply to their roots or other parts is greatly reduced depends upon physiological or structural differences or both. Important physiological differences which make this possible are oxygen requirement, nature of the respiratory system, and type of root system.

OXYGEN REQUIREMENTS OF DIFFERENT SPECIES OR VARIETIES

Cannon (1925) found that the roots of most of the 30 some species studied required as little as 0.5 per cent oxygen in the soil for survival, at least for a limited time, but needed two to eight per cent for maximum growth, depending upon the species and the conditions under which they were grown. When oxygen was removed completely from the soil in which the plants were growing, growth ceased in all species.

Free (1925) found that when the air in the soil of potato (*Solanum*

tuberosum var. Salinas-Burbank) was replaced by cylinder nitrogen containing 0.5 per cent oxygen, the plants immediately showed serious injury, characterized by wilting, death and decay of the roots, and final death of the plants.

Girton (1927) showed that the elongation of tap and lateral roots of sour orange seedlings in sand cultures was entirely suppressed by a concentration of 1.2 to 1.5 per cent of oxygen in the soil air and that retardation was evident with five to eight per cent oxygen at 28° C.

Boynton, De Villiers and Reuther (1938) stated that apple tree roots larger than 1 mm. in diameter were able to survive for a considerable period of time in a soil atmosphere containing less than 0.1 per cent oxygen when the trees as a whole were in active growth. They concluded from controlled greenhouse experiments with apple seedlings that when the oxygen in the soil was maintained at three per cent, the roots were at a "subsistence level" with respect to oxygen, that is, they continued to live but grew slowly if at all. They found also that a high oxygen level appeared to be necessary for the initiation of new roots from an existing root system and that normal growth of existing root tips did not occur below ten per cent.

Childs (1941) found no appreciable depressing effect of a reduced oxygen supply to apple roots on their growth until the concentration in the soil air was slightly less than 12 per cent, when a distinct drop was noted. Growth was gradually depressed as the oxygen content of the air was reduced until a concentration of one and one half to two per cent was reached. Further reduction in the oxygen concentration resulted in a second distinct drop in growth. Childs states that "When the concentration of oxygen about the roots was less than 1½ per cent the fibrous roots were dead, the larger roots very dark in color and there was no new growth of any kind".

Shive (1941) stated that the optimum oxygen concentration for the growth of soybean plants in culture solution was approximately six p.p.m. Below that optimum the plants showed oxygen deficiency symptoms, above it they showed oxygen toxicity. The increase in dry weight of oat plants was directly proportional to the concentration of oxygen in solution up to eight p.p.m. At a concentration of 16 p.p.m., the average increases obtained were considerably smaller than those obtained at eight p.p.m. Tomato plants showed marked increase in growth with increased oxygen supply, the greatest increase being obtained at a

concentration of 16 p.p.m. Similar results were obtained by Gilbert and Shive (1942).

Boynton and Compton (1943) showed that a decrease in the dissolved oxygen content of the nutrient solution to approximately six p.p.m. caused a marked reduction in the number and weight of new roots and in the top growth produced by apple, prune and peach trees.

Seeley (1949) found that rooted cuttings of rose, var. "Better Times", in soil aerated with a gas mixture containing one per cent oxygen produced only a little new shoot growth and showed foliar chlorosis. The root systems were nearly or entirely dead at the end of the experiment. Cuttings in soil aerated with five per cent oxygen made fairly good growth, and, although shoot growth was slightly reduced, no specific oxygen deficiency symptoms were apparent. The root systems were good but were not so extensive as were those of plants in soil aerated with 10 and 21 per cent oxygen. The greatest root and shoot development was made by cuttings in soil aerated with 10 and 21 per cent oxygen. The difference in growth between the two treatments was not significant.

Leonard and Pinckard (1946) obtained apparently optimum growth of cotton seedlings at 28° to 30° C. in nutrient solution cultures aerated with air mixtures containing 7.6, 10, 15 and 21 per cent oxygen, respectively, with ten per cent carbon dioxide and the remainder nitrogen, in all mixtures. Roots did not grow at oxygen concentrations below 0.5 per cent but the roots remained white and appeared not to be injured. When the gas mixture was replaced by air containing 21 per cent oxygen, normal branch roots developed and sometimes began to grow again. Root growth was only a little less when a gas mixture containing five per cent oxygen was passed through the nutrient solution than was obtained when 7½ per cent oxygen was used. The concentration of dissolved oxygen varied from 2.7 p.p.m. in the solution through which air containing 7½ per cent oxygen was passed up to 7 p.p.m. in the solution aerated with air containing 21 per cent oxygen.

Curtis (1949) found that both avocado and citrus seedlings grown in nutrient solution showed oxygen deficiency injury at a concentration of 0.7 p.p.m. or less. The lowest concentration at which injury did not occur was one p.p.m. Curtis stated, "Evidently the critical concentration lies somewhere between 0.7 and 1.0 p.p.m. . . . As the oxygen concentration increased root growth showed improvement, both during and

after treatment, until an oxygen level 8.0 to 8.6 p.p.m. was reached". Root growth of both avocado and citrus seedlings decreased at higher oxygen levels.

Curtis and Zentmeyer (1949) showed that avocado seedlings were not visibly injured by concentrations of oxygen as low as 0.9 p.p.m. in the nutrient solution. Seedlings were not permanently injured when kept at this level for two days but were severely damaged and did not recover when returned to full aeration after being subjected to this concentration for four or more days.

Vlamis and Davis (1943), using barley seedlings growing in flasks through which air containing known concentrations of oxygen were passed, observed that root and shoot growth of the seedlings decreased rapidly at oxygen concentrations below 9.5 per cent. The amount of growth was very small at one per cent and growth ceased at 0.2 per cent oxygen. The growth of rice roots was reduced at oxygen concentrations of 5.2 per cent and below but considerably less than that of barley.

Temperature is very important in determining the extent to which the oxygen supply to roots or other parts can be reduced without causing injury. Plants are able to endure low oxygen levels even for quite prolonged periods without showing symptoms of disease when temperatures are low, since less oxygen is needed at low temperatures than at high ones. Coville (1910) observed that submergence of the roots of the swamp blueberry (*Vaccinium corymbosum*) during the dormant period was not injurious but that they require a well aerated soil during the growing season. Bailey, Franklin and Kelley (1950) also state that "Blueberry plants will tolerate flooding from the first of November to the first of April. At other times surplus water is always harmful".

Dorsey and Ruth (1930) noted the absence of injury to apple trees in an orchard which was flooded at intervals from early October to the end of January. In the following spring very few trees were killed except in the lowest corner of the orchard where a drop in temperature to $-22°$ F., in January, was thought to have been responsible for the death of the trees rather than the high water.

Heinicke (1932) found that with McIntosh apple trees "The roots could be submerged from late fall before the ground was frozen to late spring after the ground was thawed out without noticeable injury" but that "Damage was likely to be severe if the trees remained in

the water for more than two weeks when exposed to high temperatures or other conditions that caused excessive transpiration". He found that with trees that were flooded after the leaves were fully open, "The foliage might remain normal for more than a month, but when there was a single day with high temperatures the leaves showed very serious injury within a few hours time". Heinicke stated that "High water tables are most likely to occur on poorly drained soils in the spring. . . . The first organs to suffer are the flowers. . . . Sooner or later the leaf and shoot also begin to show injurious effects".

The extent to which the oxygen supply to fruits and vegetables in storage or transportation can be reduced without causing injury is also affected by temperature. Platenius (1943) found that "There was evidence that the tissue became more tolerant to low oxygen with aging and with a lowering of the temperature".

The difference between the concentration of oxygen required by plant roots for optimum growth and that for survival of a particular species of plant at a given temperature represents the range of oxygen deficiency for that species. Cannon (1925) stated that "This range is apparently specific and is related to the aerobism of a species, being greatest in those most dependent on a good oxygen supply". Cannon pointed out that the range of oxygen deficiency in orange and willow is small, probably not greater than 1.5 per cent, whereas in *Zea* and *Pisum* the range is relatively large. Cannon also stated that "the oxygen content of different soils, as now known, is of such magnitude as to come within the upper critical concentration for root growth in plants".

The rate at which oxygen is supplied to the roots may be a decisive factor. Free (1925) stated that "Plant roots apparently can use oxygen from atmospheres of great dilution. . . . the only important matter appears to be that oxygen be supplied at a sufficient rate. A very small percentage in the atmosphere is sufficient if the atmosphere is changed rapidly enough. Accordingly, any determination of "oxygen requirement" for roots, ... is really a determination of minimum rate of supply, not of minimum percentage or partial pressure".

These statements, however, apply only to soils of normally good structure with a moisture content at or below normal water-holding capacity. In fine-grained soils, and often also in soils with a structure that normally provides good aeration, the rate of supply of oxygen may not be sufficient to meet the minimum oxygen requirement, at least of

certain plants, as was pointed out previously. In poorly drained or flooded soils, the rate of oxygen supply, because of its dependence on the rate of diffusion through water, is often too slow to satisfy the minimum requirement of a particular plant unless the plant is adapted anatomically to life under such conditions.

DIFFERENCES IN THE NATURE OF RESPIRATORY SYSTEMS

Another important physiological difference which enables plants to survive a period of oxygen deficiency is in the nature of the respiratory system. Marsh and Goddard (1939) presented evidence of the operation of two respiratory enzymes in carrot, one of which accounted for most of the respiration of the root and young leaves, the other for only a fraction of the respiration in these parts but accounted for all the respiration of mature leaves. Evidence that the nature of the respiratory systems may change with age was supplied by Merry and Goddard (1941) who found that cytochrome oxidase, an important respiratory enzyme in young leaves of barley, is absent or is not essential for the respiration of mature leaves.

DuBuy and Olson (1940) observed that, in the coleoptile of oats, a critical point in the respiration process, below which a new and lower rate persists, occurs at a definite low oxygen concentration; they concluded that there are two respiration systems, "one of which might be the cytochrome-indophenol-oxidase system and the other some cyanide insensitive system such as is associated with the action of the yellow ferment or flavin enzyme".

Laing (1940a) found that rhizomes of *Nuphar advenum, Nymphaea tuberosa* and of other hydrophytes, corms of *Sagittaria* and crowns of *Asclepias incarnata* were able to respire anaerobically for long periods without appreciable injury. He found also that the oxygen content of the internal atmosphere of the rhizomes in their native habitat may at times be as high as ten per cent by volume, and concluded that they may respire aerobically at times and anaerobically at other times or that both types of respiration may proceed simultaneously much of the time.

Taylor (1942) showed that there is a fundamental difference between the respiratory systems of wheat and rice. He concluded that "The superiority of rice over wheat in ability to germinate and grow in very low oxygen concentrations is dependent upon the possession by rice of

a highly functional fermentation system that more than compensates for a respiration system that is even weaker than that of wheat".

Some plant species have a respiratory system that enables them to obtain oxygen for respiration by reduction of absorbed nitrates. Arnon (1937) found that nitrate nitrogen in culture solution relieved the offects of oxygen deficiency in barley.

Haas (1940) reported that "Two-year-old Valencia orange trees grown in heavy black soil maintained continuously in a water saturated condition died in 16 months when they were supplied with a relatively large amount of nitrogen as $(NH_4)_2SO_4$ whereas trees grown under similar conditions and receiving the same amount of nitrogen as $Ca(NO_3)_2$ were still alive and were able to recover after the soil was drained".

Shive (1941) showed that soybean grown in nutrient solution of very low oxygen content, or in which there was no oxygen, could persist for considerable periods with growth rates much below the optimum and could even reproduce under these conditions, although very poorly. Evidence indicated that this ability depended upon use of oxygen obtained by reduction of nitrates in the root tissues. Nitrate absorption, and also its reduction in the root tissues, were greatest at the lowest oxygen concentration, and both became low at higher concentrations of oxygen in the nutrient solution.

Gilbert and Shive (1942) concluded that the much more rapid increase in dry weight with increasing oxygen supply to the roots of tomato and oats over the range of zero to four p.p.m. as compared with the small increase from four to 16 p.p.m. was undoubtedly due to the fact that under deficient oxygen supply the rate of absorption of nitrate from the nutrient solution and its reduction in the root tissues were high, thus providing a source of oxygen to supplement the external supply.

Gilbert and Shive (1945), in experiments with oats, soybean and tomato, pointed out that when the plants were transferred from a nutrient solution, in which the oxygen in solution was at equilibrium with that in the air, to solutions of low oxygen concentration, the plants changed from an aerobic to an anaerobic type of respiration. They stated that this "change occurs more rapidly with oat roots than with soybean. The tomato also responds more rapidly than the soybean to low O_2 conditions".

Bain and Chapman (1940), however, in experiments with avocado and grapefruit seedlings in soil cultures, found no evidence that addition of nitrate to waterlogged soils was of value in compensating for a deficiency in the oxygen supply to the roots. On the contrary, nitrate was definitely harmful to both avocado and grapefruit.

STRUCTURAL DIFFERENCES

The presence of an aerating system, through which the oxygen required by roots is supplied by diffusion from the aerial parts of plants, has been assumed very generally to account for the ability of rice and various marsh plants to grow in habitats in which the amount of oxygen present is very small or is entirely lacking. Evidence in support of this assumption has been presented by several investigators. Van Raalte (1940) demonstrated by analysis of the gas from air spaces in roots of rice that the plants are able to obtain their supply of oxygen from the leaves and concluded that they depend entirely upon this source of supply. He showed that there is a gradient in the oxygen concentration from nine to 11 per cent in the basal portion of the roots to 2.1 to 8.1 per cent in the tip portion. He found, however, that the oxygen concentration in the roots was not increased by photosynthesis.

Conway (1937) showed that the gas from the air spaces in roots of *Cladium mariscus* attached to the plant had an oxygen content of slightly over 17 per cent, even when the roots, rootstock and bases of leaves were submerged in water with a dissolved oxygen content of 0.48 mg./L, but that the oxygen content was very low in excised roots.

Laing (1940b) made analyses of the oxygen and carbon dioxide content of the internal atmosphere from the petioles, culms and rhizomes of *Nuphar advenum*, *Peltandra virginiça*, *Pontederia cordata*, *Typha latifolia*, *Sparganium eurycarpum* and *Scirpus validus*. He stated that "In all these species, the presence of an oxygen gradient from the leaf to the rhizome, with the highest point in the leaf on a sunny day, definitely shows that the oxygen produced in photosynthesis diffuses into the rhizome, and the carbon dioxide, which also has a gradient, but in the reverse order, diffuses into the leaf and is there used in photosynthesis".

Vallance and Coult (1951), in a study of the oxygen supply to roots of *Menyanthes trifoliata*, found that when the plants were kept in darkness, with the roots in nitrogen and the stems and leaves in air, the

intercellular spaces of the roots contained from 13.5 to 17.5 per cent oxygen. The part of the stem adjacent to the roots contained 14 to 18 per cent oxygen. When the tops of the plants were in nitrogen and the roots in air, the concentration of oxygen in the roots fell to 3.1 per cent or less in three plants and to six per cent in a fourth one. The major part of the air supply to the roots was thought to be transported to them through the stellar air passages.

Scholander, Van Dam and Scholander (1955) made a study of the respiratory gas exchange in the roots of two mangroves, *Avicenna nitida* and *Rhizophora mangle*. The soft, spongy radial roots of *Avicenna* are embedded in mud which was found to be completely free of oxygen. Numerous air roots extend upward from the radial roots. The air roots above the mud are covered with lenticels, especially toward the apex, thus providing a passage way for the exchange of air between the external atmosphere and that of the radial roots. Air exchange through the lenticels of the air roots was "basicly a continuous process, modified by the tide but not primarily caused by the tide". The oxygen concentration in the radial roots was often as high as 15-18 per cent, although in roots in deeper water the oxygen content was often lower.

Aeration in *Rhizophora* is accomplished by means of stilt roots which extend downward from the trunk of the tree. At the lower end of the stilt roots is a bunch of spongy, gas-filled roots embedded in oxygen-free mud. Numerous lenticels are on the stilt roots, through which there is direct communication from the lenticels to the mud roots. The oxygen content in the mud roots was maintained at 15-18 per cent but showed a diurnal variation. Plugging the lenticels with grease caused the oxygen content of the air in the mud roots to drop two per cent or less within two days.

The possibility that oxygen liberated in photosynthesis may supplement atmospheric oxygen in aeration of roots was suggested by Cannon (1925). Cannon observed that corn, growing in soil, appeared to be more tolerant of an oxygen deficiency during sunshine than during a preceding period of cloudiness. He suggested the possibility that oxygen may diffuse from the shoot to the root when there is very little oxygen in the soil. Cannon (1932) found also that when the roots of sunflower plants or the cut ends of excised leafy branches of apricot were placed in oxygen-free distilled water, the oxygen content of the water increased when the shoots were exposed to sunlight.

Other evidence also suggests that oxygen may be supplied to roots from aerial parts of plants, even though the cortex of both roots and stems consists of cells compactly arranged. Glasstone (1942) demonstrated that in 17 species tested, air under slight pressure was able to pass through their tissues either from leaves to roots or from roots to leaves. In some plants, particularly tobacco, very high rates of passage of air were observed with almost undetectable differences of pressure.

Sartoris and Belcher (1949) found that sugar cane was able to survive long periods of flooding if the growing point of the stalks was not submerged. Plants of all varieties of sugar cane deteriorated rapidly after being completely submerged for several days, and, without exception, submerged plants died. Similar observations were made by Stevens (1948).

Observations by Brown (1947), in experiments with seedlings of squash (*Cucurbita pepo*), make it appear probable that a transfer of gases from shoot to root, or reverse, may sometimes occur by means other than diffusion. Brown observed that "In normal intact seedlings of Cucurbita in which both the root and shoot are exposed to air, nitrogen is continuously lost from the root in considerable quantities. . . . It was also found. . . . that an outflow of hydrogen and oxygen occurred when these gases were supplied to the shoot but not to the root". With any gas used the outflow of gas from the root ceased when the hypocotyl was severed or the cotyledons removed. Brown stated that "current concepts of simple diffusion through the intercellular space system of the plant proved to be completely inadequate" to explain these facts, and that it appeared to be necessary to assume "the existence of some mechanism for the active translocation of gases in solution". The path of flow was not determined, but evidence indicated that it might be either through the parenchyma or the vascular tissue, with the possibility that the phloem might be the primary channel of transport.

DIFFERENCES IN TYPES OF ROOT SYSTEM

Some species of plants are able to survive prolonged periods of flooding by having a naturally shallow root system, or by the development of adventitious roots when the original roots are killed by submergence. Many species characteristically develop a shallow root system. Howard and Howard (1920) mentioned roselle (*Hibiscus sabdariffa*) as being a "surface-rooted" species, and that some varieties of *Hibiscus*

cannabinum and *Crotalaria juncea* also are shallow-rooted. Other examples might be given also.

Most seed-bearing plants, however, have deep-growing root systems, but many species have the ability to develop adventitious roots near the surface if the original roots are killed by flooding or other means. Bergman (1920) found that when the roots of *Pelargonium zonale*, *Phaseolus vulgaris* and *Impatiens sultani* potted in soil were submerged, the plants soon wilted but could be restored to normal if air was supplied to the roots. After a week or ten days all plants developed new roots at or near the surface, after which the plants were able to live and grow without having air or oxygen supplied artificially.

Cannon and Free (1920) observed that "When a plant of the ordinary sunflower is grown in soil which is normally aerated, and is then placed under conditions in which the normal soil air is replaced by nitrogen, the roots previously developed die. New roots immediately start from the lower end of the stem and replace the previous root system. If transpiration is low, it will survive this change of root systems, and continue to live apparently healthily, under anaerobic conditions in the soil".

Emerson (1921) found that the roots of many bog plants were restricted to depths of six cm. or less and were always above the water level. Roots and stems of cranberry (*Vaccinium macrocarpon*) died at the surface of the water. (*Larix laricina*), a very common representative of bog communities, had no tap root; all the roots were horizontal and near the surface.

Dean (1933) found that plants of *Acorus calamus, Hibiscus militaris, Sagittaria latifolia* and *Typha latifolia*, grown in three types of soils—coarse sand, colloidal clay, muck—all ten inches in depth and covered with six inches of water, developed shallow surface root systems, whereas with aeration the roots grew through the soils with the greatest growth in the region of the aerating coils. "*Typha latifolia* displayed the greatest adaptation to growth in stagnant soils by the development of finely branched water roots. This is evidently a response for securing oxygen peculiar to this plant, as water roots were rarely observed in aerated cultures. The occurrence of water roots probably accounts for the fact that *T. latifolia* plants grew in unaerated clay and muck". "The water roots originated at the highest point of the basal node and grew up and out upon the soil surface. . . . These roots correspond to the

superficial adventitious roots observed by Emerson (1921) on *Alnus* and other land plants growing in swamp land, and by Weaver and Himmel (1930) on *Typha latifolia* in their water-saturated cultures".

Sartoris and Belcher (1949) observed that "When the stalks of sugar cane plants are flooded one of the first responses is the growth of roots on the submerged nodes. . . . Varieties that failed to survive produced nodal roots sparsely or not at all".

Kramer (1951) found that tomato plants growing in soil in pots which were submerged in water to a depth of one to two inches above the soil surface developed numerous adventitious roots after six days but that relatively few roots developed on plants when the pots were sunk in soil and then flooded. Plants in pots submerged in water developed extensive root systems and were growing and flowering after 12 to 14 days of flooding. Sunflower plants under the same conditions began to form adventitious roots on the second or third day after they were flooded, and after a week had developed good adventitious root systems. In contrast to tomatoes and sunflowers, very few tobacco plants formed adventitious roots, and after a week the roots and most of the submerged part of the stems of all flooded plants were dead, whether the pots in which the plants were growing were submerged directly in water or were sunk in sand or soil and then submerged.

Alberda (1953) found "that rice plants in the field develop a superficial mat of fine, abundantly branched roots at the surface of the soil" and concluded from experiments that "Development of a root mat at the soil surface facilitates oxygen transport to the rest of the root system but does not necessarily imply that other ways of oxygen supply are completely blocked". Alberda stated also that Harrison and Aiyer (1913) "mention that in their pot experiments rice developed a more superficial root system in undrained pots than in drained ones" and that Sethi (1930) "also observed the development of a superficial layer of fine roots". Alberda also pointed out that "Although several authors have connected this layer of fine, abundantly branched roots at the surface of the soil with the oxygen supply of the rice plant, no definite proof of such a connection has yet been given".

Evidence presented by various investigators indicates that rice is adapted in three ways to growth in poorly aerated soils: *a)* structurally, in having a well developed aerating system, as shown by Van Raalte (1940); *b*) by the nature of the respiratory system, as shown by Taylor (1942);

c) by a special type of root system, as pointed out by Harrison and Aiyer (1913), Sethi (1930) and Alberda (1943). Other plants also are known to have more than one way by which they are adapted to growth in poorly aerated soils. However, further studies on the relation of plants to growth in poorly aerated soils are necessary.

SUMMARY AND CONCLUSIONS

Consideration of the many factors involved in the occurrence of diseases in plants growing under conditions of oxygen deficiency and of the various interrelations of these factors makes it evident that the problem of oxygen deficiency as a cause of disease in plants is a very complicated one, the significance of which has not been generally recognized. As a result, in studies to determine the effect of oxygen deficiency on plant growth and productivity, consideration has been given, usually, only to very few, often not more than one or two, of the factors involved.

Failure to consider all factors concerned in the occurrence of diseases caused by oxygen deficiency has led often to conflicting results and erroneous conclusions. This, however, can be said to be a fault only of some of the more recent studies. Early studies were exploratory in character and were concerned only in establishing the need of an adequate oxygen supply to roots for their proper functioning, and in determining the extent to which the oxygen supply in soils under various conditions is sufficient for normal plant growth. These studies not only established the need of adequate aeration for plant growth but also revealed the great economic importance of good aeration of soils in agriculture and forestry, and of good ventilation of fruits and vegetables in transportation and storage. It seems, however, that in later studies the relation of aeration to normal functioning of plants would have been considered with reference to more of the factors concerned than has been done. Some of the later studies have shown much improvement in this respect, but no study has yet been made in which all the factors have been considered.

One important reason for differences in the results obtained by different investigators is that concentrations of oxygen, or of carbon dioxide, in soils either were not determined or were not established with certainty. The macro-methods of gas analysis generally used do not provide dependable data, as was pointed out by Blake and Page (1948),

Raney (1949), Taylor (1950) and others. Although newer methods giving apparently more reliable results are available, little use has been made of them. Further studies of the oxygen and carbon dioxide content of soils are necessary.

Concentrations of oxygen and of carbon dioxide in nutrient solutions also were not always known. Aeration has often been at too low a rate or for insufficient time to maintain the oxygen content of the solutions at a level adequate for the plants used. The rapidity with which the oxygen content of nutrient solutions may be reduced and the extent of reduction was pointed out by Allison and Shive (1923) and by Arrington and Shive (1936). The inadequate aeration often provided may have been due to the failure of many investigators to realize that the solubility of oxygen in water is relatively low and decreases as the temperature of the water increases. Water at 0° C., in contact with the atmosphere, will absorb only 10 cc., or 1.43 mgs. of oxygen per liter, or 14.3 parts per million. This amount is only about five per cent of that in air. On the other hand, the amount of oxygen consumed by plant roots, or by microorganisms in the soil, increases as the temperature rises; and, because of the extremely low rate of diffusion of oxygen through water, a deficiency of oxygen may occur in the immediate vicinity of roots as various investigators have assumed.

Carbon dioxide, because of its much greater solubility in water as compared with that of oxygen, may reach a relatively high concentration, especially near roots, as suggested by Hole (1918), Garrett (1936), Leonard (1945) and others, although this has not been established by analysis of soil air or of culture solutions in the immediate vicinity of roots. Analytical methods previously available are not suitable for such determinations.

Consideration of these facts makes it clear that dependable results concerning the effect of an insufficient supply of oxygen to the roots of plants in nutrient solution can be obtained only when the oxygen and carbon dioxide concentrations in the air current used for aeration are known and the rate of aeration is sufficiently rapid to maintain the desired concentrations of these gases in the nutrient solution in accordance with the partial pressure of the respective gases and their solubility at given temperatures. Furthermore, analyses to determine the concentration of these gases in the nutrient solution should be made to establish that the required conditions are satisfied.

In experiments with plants grown in soils, also, the concentration of oxygen and of carbon dioxide in the air current used for aeration must be known, and the rate of flow of the air current through the soil must be sufficiently rapid to maintain the desired concentration of these gases throughout the soil. Maintenance of a uniform concentration of the gases used, in all parts of the soil, may be difficult because of the tendency of an air current flowing through a soil to make a channel through the soil and thus cause the effect of aeration to be lost.

In many of the studies to determine the effect of carbon dioxide on root growth, absorption of mineral nutrients or other physiological processes, carbon dioxide only was passed through the soil or nutrient solution used. Accordingly, the results obtained represent the effect of exclusion of oxygen, upon which is imposed that of carbon dioxide; they do not indicate the effect of carbon dioxide in the presence of sufficient oxygen to satisfy at least the minimum requirement of the plant and part used. Results obtained by such methods cannot be accepted as conclusive. Fortunately, numerous experiments have been made with various concentrations of carbon dioxide in the presence of known concentrations of oxygen. Such experiments have shown that carbon dioxide, except at concentrations rarely found in soils, very generally have no important effect on growth of roots, absorption of mineral nutrients, or other physiological processes. Nevertheless, even under these conditions, variation in the extent to which different species are affected by various concentrations of carbon dioxide has been observed.

Further studies on the relation of the oxygen and of the carbon dioxide content of a soil to infection of roots by parasitic fungi are needed also. Although a considerable number of studies of the relation of oxygen and carbon dioxide concentrations to the growth of various fungi in cultures have been made, the effect on roots of a host plant of different concentrations of these gases, usually were not considered; both are necessary. Such studies should be made, if possible, under field conditions or at least under experimental conditions reproducing as nearly as possible those existing in the field. With analytical methods now available this should be possible.

Another reason for the diverse results obtained by different investigators in studies of the effect of various concentrations of oxygen or of carbon dioxide on growth or other physiological processes is that

different kinds of plants may have very different respiratory systems. Difference in the nature of the respiratory system may be a very important factor in determining the ability of a species to survive a period of oxygen deficiency, and is a factor that often has not been taken into consideration. Our knowledge of respiratory systems in plants and of their relation to the effect on different kinds of plants of a deficiency in the oxygen supply to plant roots or other parts, and to the ability of plants to survive a period of oxygen deficiency, is very scant. Further studies on this relation are necessary.

The effects of reduced compounds, for example, nitrites, sulfides and ferrous iron, in the soil under anaerobic conditions are secondary; ordinarily, they would not be present in appreciable amounts in a well aerated soil. Hence, any effect that they may have is not to be considered as the primary cause of injury or death to plants. However, in plants which, because of physiological or structural differences, are able to grow in a soil deficient in oxygen, nitrites or other reduced substances may be the cause of injury or death to the roots or to the entire plant. No data with reference to this are available.

The means by which a deficient supply of oxygen to roots or to other parts of a plant affects growth or other physiological processes, and by which, in the absence of oxygen, ultimate death is caused, remains to be determined. The ability of plants to survive a period of oxygen deficiency varies greatly as between species; some plants die within a few days, others survive for weeks or months, or, in some species of trees, even for several years, but death always ensues. Various explanations as to the cause of death have been proposed. Evidence that death is caused by an accumulation of alcohol, acetaldehyde or an organic acid of any kind, has not been obtained. The assumption that death is due to a lack of metabolic energy resulting from interference with the respiratory process, as suggested by Grünberg (1932), Tamiya and Yamaguchi (1933), Paech (1935) and Miller (1938), is much more plausible.

It appears probable that the interference occurs at the final stage of the respiratory process, since it is at this stage that the energy, or most of it, necessary for processes concerned in growth, or that is necessary even for survival, at least in some species, is released. Some plant species have a respiratory system with alternate pathways which provide energy for metabolic processes under anaerobic conditions. In such spe-

cies interference with the terminal stage of respiration means only that respiration is changed from an aerobic to an anaerobic type, as has been demonstrated for a number of plants. It appears probable, also, that the early death of other kinds of plants in the absence of oxygen means that, in these plants, the only source of energy is that released in the final stage of respiration. The relation of the respiratory system of a plant to its ability to grow or to survive under conditions of oxygen deficiency appears to be a fertile field for study.

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CHEMICAL CONTROL OF CEREAL RUSTS[1]

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INTRODUCTION

Historically, the concept of chemical control of plant diseases evolved from observations on the effect of various compounds on the incidence of disease. The account of the earliest use of sulfur is a good illustration (114). The basis for the concept was associated closely with the experimental establishment of the primary cause of fungal disease by Prevost

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(146) who also used copper sulfate to control the bunt of wheat. The elucidation of these basic ideas of parasitism by DeBary (35) and of disease control by Kühn (101) and the demonstration of the effectiveness of Bordeaux mixture in disease control by Millardet (120) placed chemical control of plant diseases on a sound basis and initiated a multitude of tests on fungicides, many of which were directed toward the control of cereal rusts. From 1891 through 1894 numerous tests were conducted in the United States (14,15,49,80,81,135,136) and in other widely scattered locations throughout the cereal-producing areas of the world (30,39,132,194). Although some control of cereal rusts was obtained with sulfur, copper and other compounds, these early investigators generally emphasized the economic impracticability of chemical control of these diseases. Chemical control of the powdery mildew of cereal crops has been on essentially the same economic basis as the rusts, although the predominantly surface position of the pathogen perhaps would indicate easier control (201).

Emphasis was shifted from chemical control to the use of rust-resistant varieties for a period of two decades. The rediscovery of Mendel's laws of heredity in 1900, the establishment of disease resistance on a genetic basis by Orton in 1900 (133) and the demonstration of the factorial inheritance of rust resistance by Biffen (13) and Nillson-Ehle (131) presented a different and seemingly more economical method of disease control. The contrast in the economics of control, i.e., between the use of rust-resistant varieties and the frequent applications of protectant fungicides, was important in stimulating this shift in emphasis away from chemical control of rusts (68).

Realization that physiological races of the rust pathogens limit the permanence of resistant varieties again renewed interest in chemical control. The early reports by Eriksson (38), Ward (188), Stakman (175) and others on the physiological specialization of the rust pathogens did not fully reveal the role of specialization in determining the permanence of resistant varieties until some 20 years later. Also, advancements in fungicide and insecticide chemistry and means of application were factors in starting renewed investigations in chemical control of cereal rusts. The initiation of extensive tests, especially in Canada in 1928, perhaps was associated with the onslaught of stem rust on the fine quality, hard red, spring wheat, Marquis. Similarly, stem rust and leaf rust were causing heavy losses in wheat in Russia

and in southern Europe, and chemical control again was investigated as a means of protection of the wheat crop. Investigations on chemical control of cereal rusts have expanded greatly, both in the search for an economical fungicide for rust control and in the initiation of basic studies on the physiology and chemistry of fungicidal action (57,115, 117) and on the physiology of parasitism (1,2,34,77,100,162). These investigations have been stimulated and directed also by parallel studies of chemical regulation of growth (105,148,174,181).

This review of the literature on chemical control of cereal rusts is presented under the several groups of compounds investigated, arranged, in part, in historical sequence. The pertinent more recent literature on the physiology of parasitism and growth is reviewed, especially where associated with the suggestion of new chemicals or the elucidation of the physiology of their action. In the recent investigations on systemic-acting compounds, much of the advancement of knowledge has been in relation to insecticides and herbicides; therefore, important review articles from these fields are included.

INORGANIC SULFUR COMPOUNDS

As stated in the introduction, the protectant fungicidal value of sulfur was recognized early in the history of plant pathology (114). In the experiments conducted between 1891 and 1894 (14,15,30,49, 80,81,93,101,132,135,136,194), inorganic sulfur compounds, principally elemental sulfur, were tested extensively and found erratic in behavior and uneconomical for rust control. Both the physical state of the sulfur and the methods of application were responsible for the generally poor control. The second series of tests with inorganic sulfur, starting about 1925, were made with more diverse preparations, including finely divided and colloidal sulfur preparations and spray and dust applications. The Canadian experiments under the leadership of Bailey (7-9), Greany (59-64) and others (20,32) were the most extensive. These were paralleled by more limited tests at the New York, Minnesota and other Experiment Stations (4,23,24,88,96,97, 102,103,110,189,191). Similar evaluations of inorganic sulfur and other compounds were in progress in southern Europe (11,36,55,79, 118,125,137,138,139,168-171), Russia (19,67,95,98,108,126,151,154, 165-167,202) and other locations (22,122,128,143). Sulfur, sulfides, sulfates, Bordeaux mixture and other compounds were evaluated for

rust control and phytotoxic action. The more recent investigations on the influence of ferric sulfate in inhibiting rust susceptibility induced by dilute solutions of zinc, cobalt and manganese salts, and the killing of mycelium in the established uredia, suggest further study of inorganic salts and their action both as fungicides and as inhibitors of physiological processes (46,57,115). The mechanism of fungicidal action of sulfur has been reviewed recently by McCallan (115). The mechanics and number of applications required and cost of application and materials, when compared with minor increases in yield of grain and quality, again demonstrated the uneconomic use of sulfur on cereal crops (63,68).

ORGANIC SULFUR COMPOUNDS

The discovery in 1934 by Tisdale and Williams (180) of the fungitoxicity of the dithiocarbamic acid derivatives apparently initiated investigations on the organic sulfur compounds. The three important fungicidal groups of the carbamates are: *a*) metallic dithiocarbamates, *b*) thiuram disulphides and *c*) bisdithiocarbamates (115). The zinc, iron and manganese salts of these compounds have been shown to be good protectant fungicides for rust control, but from three to eight applications were necessary to obtain control (5,16,17,47a,69,109,134, 142,155,159,173,196). The importance of the carbamic acid esters as systemic insecticides (119) suggests further investigations with this group of compounds.

Apparently, Gassner and Hassebrauk (52,53,72,73) were among the first to test a wide range of organic compounds as rust therapeutants. The chemicals were applied generally through the soil solution at the time of inoculation, and their effectiveness was measured by the change in rust reaction. Hassebrauk (72,73) in 1938, only three years after the discovery of the efficacy of the sulfonamides in controlling bacterial infections in animals, showed by the above methods that o- and p-toluene sulfonamide and metanilic acid, 3-aminobenzenesulfonic acid, reduced rust development in wheat. Field trials with these compounds, however, were not successful (70). Hassebrauk (74) and Straib (176) later showed that these and other compounds were effective in controlling the leaf rusts of barley, oats, rye and wheat under greenhouse conditions. Other investigators (6,26,48,107,113,124,142,195,196) reported the partial effectiveness of the sulfonamides when applied to

leaves of cereals with suitable wetting agents. Hotson in 1952 (82,83,) and Hassebrauk in 1952 (76) demonstrated that the control of rust with sulfonamides can be reversed by treatment with p-aminobenzoic acid and folic acid in an action similar to that claimed for the activity of the compounds as bactericides (193). Jones, Crowdy and associates (32a,b,c;90) also have confirmed the systemic action of the sulfonamides in the control of the rust of broad bean, wheat and crown rust of oats under greenhouse conditions. Livingston (107) in 1953 was apparently the first to report on this group of compounds applied as low volume sprays with wetting agents for the control of cereal rusts under field conditions. The sodium salt of sulfanilic acid gave moderate control of rust and increased yield of grain. The salts of sulfamic acid used as sprays and dusts gave moderate control of rust under some environmental conditions, but phytotoxic action was evident. Further investigations with the sulfamates have indicated: *a*) rust control under favorable high humidity conditions, *b*) phytotoxic action especially in reduced germination, *c*) accumulation of the chemical in the grain of wheat and oats in sufficient quantity to affect quality, *d*) relatively little effect on germination and quality of barley (6,69,107,113,142 and unpublished data).

COPPER COMPOUNDS

Bordeaux mixture, copper sulfate and copper carbonate were tested extensively in both the early (15,30,49,80,81,93,132,135,136,194) and later investigations (11,51,63,118,126,137,138,139,169,170,171,197) on rust control. In general, these and other inorganic copper compounds gave poor rust control and considerable phytotoxic action on the cereal plants. The organic copper compounds tested apparently were ineffective also (46,63). The role of cysteine and other amino acids in inhibiting the toxic action of copper, mercury, etc. probably has a bearing on the generally poor control of the rusts with the fungicides involving the heavy metals (46,56,115).

MERCURY COMPOUNDS

Mercury compounds, like those of copper, have attained wide use as fungicides; however, also like copper, they have been relatively ineffective in cereal rust control (80,81,115,194).

BORON, SELENIUM, FLUORINE, IRON, LITHIUM, MANGANESE, NICKEL

The occurrence of these minor elements in plants and their uptake from the soil solution and spray application have been studied extensively, especially in relation to the direct effect on plants of deficiencies and excesses. They have been investigated also as insecticides. Metcalf (119) dates the success of internal therapy of plants for protection against insects from the report of Hurd-Karrer and Poos (84) on selenium. The investigations on 2-fluoroethyl alcohol derivatives at about the same time demonstrated the use of systemic chemical agents in pest control. Salts of other minor elements, e.g., lithium, arsenic, fluorine, nickel, chromium and boron have been tested (27,47b,55,70, 72,78,81,92a,b,94,108,132a,160,142a,176,187a). This group of compounds generally has shown little effect on rust control, high phytotoxic action and generally high animal toxicity. Several investigators have shown that zinc salts enhance urediospore germ-tube differentiation and increase rust susceptibility (46,85,115,149,163). Preliminary investigations have shown that rust susceptibility induced by salts of zinc, cobalt and manganese was counteracted by ferric sulfate, although the mechanism of the reaction has not been determined (45,46,190). They have shown also that ferric salts killed the mycelium in the established uredium (46). Further investigations of the physiological and chemical interactions of these salts that occur frequently in the cells of cereal plants appear warranted.

Recent retesting of nickel salts as protective and eradicant fungicides has confirmed Sempio's (160) early results and shown promise in rust control. Ammonia apparently prevented the fungicidal action. Applied as leaf sprays, both protective and eradicant action were of short duration. The organic complexes such as bis [N-(2-hydroxyethyl) dodecylmethylbenzylamine] nickel II chloride persisted longer than the inorganic salts (47b,92a,b,142a).

PHENOLIC COMPOUNDS

The presence of phenolic compounds in plants and their suggested role in disease resistance, as discussed by Walker and associates (183, 184,185) and others (1,2,34,53,63,91,92,129,130), has resulted in extensive tests on rust control. A large group of these compounds are extremely effective in preventing urediospore germination at very

low concentrations. However, when used as sprays or applied through the soil solution, they have been extremely phytotoxic and generally ineffective in rust control (53,63,72,73,176). Picric acid, 2,4,6-trinitrophenol and related compounds have given some control of rusts under favorable conditions (53,73,176), but none in field tests (70). Karathane, 2-(1-methylheptyl)-4,6-dinitrophenyl crotonate and isomers killed spores and mycelium in open uredia; however, under greenhouse conditions, a ring of vigorously sporulating uredia formed around the dead uredia, indicating the intercellular mycelium some distance from the open sorus, was not damaged (unpublished data). Under field conditions Karathane has given erratic results (69,142). DDT (dichlorodiphenyltrichloroethane) has increased rust susceptibility, especially in Khapli wheat (21,47,47c,87). The role of these compounds in plant metabolism and physiological processes is reviewed later.

QUINONES

The fungicidal properties of the two more important compounds in this group—tetrachloro-p-benzo-quinone and 2,3-dichloro-1,4-napthoquinone—were investigated by McNew and associates (115,117,155). Since a number of the quinones occur naturally in plants and appear to have high chemical reactivity, this group of compounds has been studied extensively for rust control. Their behavior, both as protectants and as eradicants for cereal rusts, has been erratic, especially under field conditions (37,69,142,155).

HETEROCYCLIC NITROGEN COMPOUNDS

This group of heterogeneous compounds has been investigated extensively and some have been tested for rust control. However, those evaluated to-date for rust control of cereals have not been effective either in the soil solution or as sprays (53,73). The proposed mechanism of action of these compounds on the enzyme systems may be prevented through their inactivation by the cereal plant metabolites (56,115).

OXINES OR 8-QUINOLINOLS AND DERIVATIVES

The oxines have not been tested extensively as rust protectants; however, those evaluated have not been equal to the carbamates and, like them, require several applications (115).

OTHER ORGANIC COMPOUNDS

Several organic acids, alcohols, esters, oxides and other compounds not included in the former groups have been tested for use in rust control. Most of these compounds have been unsuccessful or only partially successful as rust fungicides. Some of the amino acids suggest possible carriers of rust therapeuticants; others, such as cysteine, inactivate the toxicity of many compounds; some change host metabolism to prevent rust development; and specific amino acids appear to inhibit spore germination and rust development (33,47,47d,53,56,72,73,77, 104,115,144,145,155a,162,164,176,177,205). Paraformaldehyde has been tested with no control indicated (53,137). Hydrocyanic acid and salts have been investigated in limited tests (53,158,197). Captan (N-(trichloromethylthio)-4-cyclohexene-1,2-dicarboximide) has reduced rust development in field tests, although the results have been erratic (69). Some sugars and sugar alcohols have been shown to reduce rust development in excised leaves floated on the solutions of these compounds (53,73,172,178). The investigations on the effect of ether, chloroform and similar compounds on rust reaction have indicated either no effect or increased incidence of rust and drastic physiological disturbances in the hosts (54).

ANTIBIOTICS AND DERIVATIVES

Investigations on antibiotics and the use of antibiotics as protectants or eradicants of plant pathogens have increased greatly during the past decade. Their use for the control of cereal rusts have been investigated extensively, although little has been published. Apparently relatively few of the large number tested have been effective in rust control. Cycloheximide (acti-dione) and derivatives have been studied extensively (43,56,69,142,147,186,187,191b,203). The results reported, as well as many unpublished data, indicate a wide range in effectiveness of control and in phytotoxic action. The acetate, oxime, semicarbazone and other derivatives of cycloheximide appear to be both less active and less phytotoxic. Some of these compounds appear to function as systemic fungicides, but the physiology of their uptake, translocation and action is relatively unknown. These results illustrate the need for more basic studies both on formulation and on the physiology of their behavior. Other antibiotics tested have not been effective in the

control of cereal rusts, although some of these have shown partial control of bean rust (32d,147,186,187,203).

HERBICIDES AND PLANT GROWTH REGULATORS

The use of some of the compounds generally classified in this category has been reported in the earlier sections. The implication of the relationship of many of the compounds in this group to rust control has been associated with the physiology of rust development and the nature of rust resistance (2,21,47,47c,77,162,164a,192). However, many growth-regulating compounds have been used directly in tests on rust control. Gottlieb and Hart (57) reported no control of stem rust under four methods of application with thiamine, riboflavin, nicotinic acid, ascorbic acid and indoleacetic acid. Control of rust with the butyl and isopropyl esters of 2,4-dichlorophenoxyacetic acid (2,4-D) has been erratic and unsatisfactory (86,140). Spraying cereal plants with maleic hydrazide, 1,2-dihydro-3,6-pyridazinedione has increased the development of the uredial stage, including urediospore production, on susceptible and moderately resistant varieties (21,47c,107,142). DDT, an insecticide discussed under phenolic compounds, also increased rust susceptibility. Both maleic hydrazide and DDT apparently increased sugars and amino acids in sprayed leaves (47c,127,164a,181, 192,204). Under conditions of low light intensity, high humidity and moderate temperature, dilute soil or spray applications of 3-(p-chlorophenyl)-1, 1-dimethylurea (monuron or CMU) and the diuron with two chlorine substitutions have controlled rust development without severe phytotoxic effects on wheat; however, these compounds have not been effective under field conditions (unpublished data and 29,,121, 142).

CHEMICAL COMPOSITION AND METABOLISM

The chemical composition of the cereal plant has been investigated both as influenced by external environment during rust development and as affected by genotype (resistant and susceptible varieties) (2,6, 50,51,52,58,76,92,123,129,144,150,177,205). The influence of composition on metabolism of rusted and rust-free plants and resistant and susceptible varieties has been studied both directly and indirectly in the search for an understanding of the physiology of obligate parasitism and of the nature of rust resistance. Unfortunately, many of

these investigations on both composition and metabolism have been conducted by comparisons of different genotypes of the cereal hosts and rust pathogens, especially in studies on the nature of rust resistance (10,77,91,92,129,144,156,177,205). While differences in both chemical constituents and metabolic processes frequently have been shown to exist, they have been general comparisons rather than specific for the interaction of host and parasite genotypes. Comparisons of the latter type are illustrated by recent investigations on corn rust (178). In investigating the influence of environment on rust reaction and the comparative metabolism of rusted and rust-free plants, specific genotypes of both host and pathogen were used. The rust reaction of one host genotype in which a single dominant gene pair conditioned rust reaction was investigated, using several clonal cultures of the pathogen, each containing one or more gene pairs conditioning pathogenicity or non-pathogenicity (necrotic fleck) for this specific host genotype. Similarly, the rust reaction of several host genotypes, each with a specific gene pair at the same or different loci that conditioned rust reaction, was studied, using a clone of *Puccinia sorghi* with one gene complex conditioning pathogenicity (41,178). Similar genotypes of flax and *Melampsora lini* have been investigated by Flor (42). Plant material of this type is available for future investigations in flax and *Melampsora lini*[2], maize and *Puccinia sorghi*, and oats and *P. graminis* var. *avenae*[3].

The entreaty is made that all future investigations on the chemistry and physiology of rust reaction be concentrated on plant materials of known genotype. The literature indicates that highly specific compounds or processes determine rust reaction. The literature demonstrates that these specific differences are not determined readily in gross material. Progress in chemical control of rust must be associated closely with an understanding of the physiology and chemistry of rust reaction.

Allen and other have reviewed the literature prior to 1954 on the

2. Dr. H. H. Flor, Pathologist, Cereal Crops Section, Agricultural Research Service, U.S. Dept. Agr., No. Dak. Agr. Exp. Sta. Fargo, N.D. can supply a series of flax varieties each containing one or more gene pairs conditioning rust reaction and cultures of *M. lini* pathogenic or nonpathogenic for these host genes.

3. The author, Dept. Plant Pathology, Univ. Wisconsin will gladly furnish similar combinations of host and pathogen for corn rust and oat stem rust investigations.

physiology of parasitism and the physiology of toxin action (1,2). The review of recent investigations on the chemical composition of cereal plants and the relation of specific groups of compounds to metabolism and rust control are included in the present paper.

The role of toxins produced by either the pathogen or the host has received attention in the rusts since Stakman's (175) definition of the hypersensitive reaction. Cytological evidence has indicated that host, pathogen or both may contribute to the reaction, depending upon the specific combination of host genotype and culture of the pathogen (42,66,106,175,178). Extracts from homogenized, germinated urediospores and from the mycelium and host tissue produced necrotic flecking on the leaves. The flecking was somewhat specific between host varieties and fungus cultures (65,71,72). Similar necrotic flecking has been reported with several compounds used as fungicides, but not so specific as in the former reactions (26,107). Recent investigations of comparative oxygen consumption by the leaves of corn inbred GG208R, inoculated with a line of *P. sorghi* that incites necrotic flecking only, and a parallel inoculation with another line that incites the fully susceptible reaction indicated that the active physiological response, i.e., oxygen uptake, of the flecked leaves initially was significantly higher than that of the rusted leaves which in turn was higher than that of the healthy leaves. The active response of the leaves with the fleck reaction subsided with the lapse of time after inoculation (178). The toxins also have been shown to be associated with differences in cell permeability (1,34,47,179).

Both the kind and amount of nitrogenous compounds occurring initially or following rust infection have been shown to vary with varieties (2,10,27,31,50,164). Application of nitrogenous fertilizers either through the soil or as foliage sprays has been shown to influence the nitrogen composition and to increase rust. Some chemicals applied as fungicides also influence the nitrogen constituents in the plant (31, 47c,d,50,144). The possible role of ammonia and of amino and amide nitrogen has been investigated both in relation to initial composition of rust resistant and susceptible varieties and in relation to changes induced by rust development and the application of chemicals (47,47b, 164,177,192,205). Ammonium nitrate was found to increase callus tissue and early mycelial growth in cultures of *Melampsora lini* on flax cotyledons (104). The data from the several investigations frequently

have appeared to present conflicting evidence, and generally they have shown little specific relation to rust development and control. However, investigations on the role of metabolites on antimicrobial agents have indicated that amino acids inactivate heavy metals, sulfonamides, many antibiotics and some toxins (56,112,115).

The investigations on the relation of mineral nutrients to rust development and control have shown that, generally, the rusts develop best on plants in a vigorous, well-balanced condition of growth. Applications of potassium- and phosphorous-containing fertilizers have indicated retarded rust development and more rapid host maturity, thereby reducing rust losses. Accumulation of phosphorous in some form in rusted leaves has been demonstrated by several methods (31,51,52). The role and nature of these phosphorous compounds have not been elucidated. Some of the chemicals used as fungicides and herbicides apparently cause, either directly or indirectly, the accumulation of potassium and other mineral salts in localized areas of the plants (31,51,52,58,164).

The relationship of carbohydrates to rust development and control has been investigated extensively. Soluble carbohydrate supplied through the compatible host medium has been demonstrated to be essential for the development of the rust pathogens beyond the initial stages of vesicle and haustorium formation. This supply may come from the seed reserves, from photosynthesis or from an external supplement to the host tissues. Allen (2) has reviewed the extensive early literature on the effect of carbohydrate supply. A wide range of hexose and pentose sugars and some alcohols are more or less effective, including some not reported in cereal tissues, although present in urediospores of a rust fungus (2,145,191a,b). Several of the systemic herbicides tested for rust control affect chlorophyll formation and carbohydrate synthesis and translocation (29,121,127,181,192,204) as well as rust development (21,47,47c,86,87,107,140).

The formation and accumulation of lipids and amorphous condensation products, especially in relation to the expression of resistance in cereal plants, have been studied extensively (1,2,66,178). These deposits generally are associated with invaded tissues, but they may be layed down adjacent to cell walls some distance in advance of the pathogen. Similar reactions and deposits frequently are associated with

necrosis caused by phytotoxic chemicals, notably the sulfamates and cycloheximide.

An extensive literature has accumulated on the effect of rust development on changes in growth factors and auxins (2,33a,34). The rather general cell enlargement or gall formation associated with the development of the haploid mycelium in initiating the aecial stage of the rust pathogens has been recorded but not investigated extensively. In the autoecious species the gall-like elevations incited by the haploid mycelium, frequently near the uredial dicaryotic mycelium which generally causes no enlargement of host cells, would indicate compounds or precursors of compounds specific to the haploid mycelium. Some of the fungicides tested for rust control, notably 2-(1-methylheptyl)-4,6-dinitrophenyl crotonate and isomers (Karathane) and sulfamic acid, when applied to open uredia of the cereal rust pathogens, cause death and discoloration of the exposed urediospores and subtending generative cells. This reaction is followed frequently by marked enlargement of the host mesophyll cells around the uredium and the development of a ring of vigorously sporulating uredia (47d).

The changes in substances stimulating the physiological processes controlled by enzyme systems and the role of the enzyme systems in the complex metabolism of this group of obligate parasites have been the subject of much investigation and extensive speculation. As summarized by Allen (2), augmented respiration is almost a universal consequence of the infection of higher plants with obligate parasites. His review of the literature and the more recent reviews by Hassebrauk and Kaul (77) and Farkas and Kiraly (40,100a) present the information pertinent to chemical control of cereal rusts. Hassebrauk and Kaul (77) have contrasted some of the enzyme systems, their action and substrates through the comparative study of Michigan Amber susceptible and *Triticum monococcum* var. *hornemanni* resistant to leaf rust grown under different environments. Kiraly and Farkas (40,100a), Sempio (162) and others have investigated the respiration rate and glycolic acid oxidase activity and other enzyme systems in rusted and healthy leaves.

These investigators have shown changes, mostly increases, in the activity of the respiratory enzymes associated with rust development (2,33a,34,40,77,99,100,100a,155a,162,164,190). Much of the initial increased respiration is contributed by the host cells (2, 34). Further

evidence in support of this assumption is illustrated by the initially high rate of oxygen consumption associated with the necrotic fleck reaction in the corn rust (page 496). Here certainly, the hypha limited to a few cells beyond the vesicle, all of which undergo rapid necrosis, cannot contribute directly to respiration although indirectly they may contribute "uncoupling" toxins (1,2,34). Accumulation of phosphorus in the infection cites and other reactions (2,31,34,47c,51,52,77) present evidence that increased use of energy-rich phosphate is associated with accelerated respiration (2,33a,34). The progressively increased magnitude of the direct oxidative pathway in rusted tissues over those of the healthy as the parasite develops to sporulation suggests that it is responsible in part for the higher rate of respiration through a hexose-monophosphate shunt (34). The inhibition of the Pasteur effect by the parasite is generally accepted (2,34). The relative host or parasite influence on the greater respiratory activity arising from infection through the hexose-monophosphate shunt or other enzyme energy release in contrast to the Embden-Meyerhof pathway in the healthy tissue is not as generally accepted (2,33a,34,40,77,100,100a,155a).

The comparative investigation of these processes will be advanced experimentally through the use of known genotypes of both host and pathogen. For example, the study of one host genotype in which a single gene pair conditions rust reaction for specific gene pairs conditioning pathogenicity and nonpathogenicity in lines of the pathogen and the parallel study of the reverse situation in which two or more genotypes of the host differing only in the gene pairs conditioning rust reaction (isogenic resistant and susceptible) for a specific line of the pathogen (41,42) represent the material suggested for future study. An illustration of this type of comparison was reviewed previously (178), in which parallel series of leaves of the inbred corn line GG208R were used with two specific lines of *P. sorghi*. The rate and total oxygen consumption ranked in ascending order were: *a*) healthy, *b*) rusted (fully susceptible reaction) incited by line 3-32; *c*) necrotic fleck (resistant) incited by line 1-20 of *P. sorghi*. A better understanding of the physiology of parasitism of the rust fungi is an essential part of basic investigations on the chemical control of rusts.

The presence of chemicals within the spores and mycelium that control the process of germination and development of the rust fungi has been investigated recently (3,44,191a,198,199,200). Information

on these internal regulators of growth and development of the pathogen is important, not only in an understanding of its metabolism but also in its control, especially in relation to systemic fungicides.

BASIC RESEARCH A PREREQUISITE TO CHEMICAL CONTROL OF RUSTS

During the past 20 years more money and man power have been invested in routine testing of chemical therapeutants in both animals and plants than in basic research on their movement and relation to cellular physiology and chemistry. In plants especially progress has been retarded materially by the meager information on entrance, translocation, chemical changes occurring after entering the plant, and the influence of environment on these processes. More progress has been made in relation to insecticides than fungicides. The explanation for this difference in progress has been discussed (18,119). Similarly, relatively little has been reported on the mode of action of herbicides (192, 204).

Investigations on the chemistry and physiology of plant development, metabolism and growth must be advanced parallel with chemical control of plant diseases. Investigations and enumeration of compounds functioning in the regulation of physiological processes and growth in plants have been reviewed frequently (105,148,181). Basic understanding of the physiology of parasitism and of disease reaction has progressed slowly (2). The investigations to-date of the complex interactions of host and obligate parasite, generally highly specific, have been conducted largely on plants of unknown and frequently unrelated genotypes or material too gross to show more than general comparisons. Recent advances in methods of experimentation with somewhat simpler physiological systems, such as clonal cultures of plant tissue grown under controlled environments, have contributed greatly to the understanding of the physiology and biochemistry of growth and development in plants. Skoog and associates (174), to cite one illustration, through the use of tissue cultures have isolated and described kinetin, a compound associated with organ formation in plants. They have demonstrated experimentally in clonal, tissue-culture systems the interaction between the growth-promoting auxins, the growth-orientating kinins and the inhibitors of each in determining both rate and form of growth. They have shown that quantitative interactions between these

factors provide a common mechanism for the regulation of growth from cell enlargement to organ formation. Use of this type of experimental approach on host and pathogen genotypes of known interaction grown under controlled environments will contribute materially to the knowledge of the chemistry and physiology of rust development and of rust control.

Information on the inactivation of chemical toxicants by plant metabolites and on the mechanism of toxicity of fungicides has accumulated for a host of compounds (18,56,112,115). Chemical and physical methods developed in relation to paper chromatography and other methods of adsorbing and eluting or isolating specific compounds have supplied the tools for further elucidation of these reactions and the isolation and identification of naturally occurring plant protectants.

The control of cereal rusts by chemicals as well as through the use of resistant varieties is associated largely with pathogens of the uredial or dicaryotic stage of this group of fungi. Three important biological phenomena are involved in determining rust reaction and rust control: *a*) the close association of the two or more genomes in the dicaryotic or binucleate cells of the fungus functions genetically in the expression of dominant or recessive characters in a manner similar to that in the diploid cells of plants (41,42,106); *b*) the uredial stage of the fungus is self-perpetuated on the cereal hosts by means of the urediospores or the fungus functions in this stage as vegetative clones; *c*) the mycelium develops intercellularly in the host tissues with haustoria entering the host cells in the intimate nutritive relationship of obligate parasitism. The origin and perpetuation of new physiological races through recombination of nuclei, gene pairs conditioning pathogenicity or through gene mutations are explained by these phenomena, and the complications associated with chemical control of cereal rusts are elucidated by them also.

In the economical control of rusts by chemicals, a fungicide must function locally or systemically through a persisting protectant or eradicant action. In the protective agent the action is directed toward prevention of spore germination and germ tube entrance into the stomatal cavity. The localized protectant fungicide must be applied to vulnerable epidermal surfaces as they unfold and persist by means of weather-resisting films or by absorption in active form into the cuticular covering of the epidermal layer. Elemental sulfur, sulfides and

dithiocarbamic acid derivatives illustrate this class of fungicides. In the localized eradicant fungicide the action commonly is directed toward killing the mycelium, especially that producing spores and the young spores in place in the uredium following the rupture of the host epidermis by the localized uredial sorus. Karathane, ferric sulfate, sulfamic acid and cycloheximide illustrate this class of fungicide. Again these fungicides are applied as sprays or dusts to the epidermal surfaces of the cereal host and their persistence in active form is an important requirement. The ideal systemic fungicide would function permanently as a protectant in preventing establishment of a pathogen without phytotoxic effect upon the host. Those studied to-date, however, function mainly as partial eradicants in retarding the rust development and sporulation. They are also generally phytotoxic and erratic in behavior under field conditions. The sulfamates, the sulfonamides and some of the herbicides are examples of this group.

As summarized in the previous paragraphs, progress in the chemical control of cereal rusts during the past 66 years has been slow. At present cereal rust control through the use of fungicides does not appear economical on a commercial basis. However, with the recent shift in emphasis from testing chemicals for rust control to expanding the basic research on the nature of the chemical action involved in rust control, it seems logical to expect that chemical control will contribute parallel with rust resistance in the prevention of crop losses.

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CHROMOSOMAL ALTERATIONS IN RELATION TO SPECIATION

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INTRODUCTION

Recent research has revealed that the relative roles of gene mutations and of other chromosomal changes in evolution have not been properly assessed in the past (16, 19, 167, 172). Data are forthcoming to indicate that the part played by the latter in evolution has been much greater than was assumed by earlier workers. It has long been implied that all strains or species originate mainly through gene mutations, phenomena which are not cytologically detectable under the microscope. Such an idea was mainly due to the fact that the available techniques could not reveal karyotypic differences between strains; they all appeared cytologically homogeneous. Lately, with improved methods for chromosome studies, such generalization has been found erroneous. Refined techniques have enabled a number of workers to distinguish strains on the basis of their karyotypes. As karyotypic differences could not be detected in earlier work because of inadequacy of techniques, over-emphasis was laid on the role of gene mutations in evolution.

Furthermore, in all plants which reproduce either principally or entirely through vegetative means, a peculiarity has recently been recorded in their chromosome behaviour (165). In somatic tissue, fixity in chromosome number has not been found in any of them investigated, and the normal 2n number has been worked out from the frequency of nuclei with the same complements. The one in the highest frequency is considered as the normal complement. Such chromosomal alterations in somatic tissue very likely have played a distinct role in the origin of some species in these genera. A new species, originating through a series of intra- and extra-cellular steps, has its initiation at the intra-chromosomal level. Changes at this level may involve a single gene, a group of genes or segments of chromosomes detectable under the microscope. Although the exact steps at the genic level have not been fully explored, it is now well established that even changes in the positions of genes are sufficient to produce distinct phenotypic effects. The phenotypic changes arising out of structural changes and rearrangement of chromosome segments are also attributable to "position effect" in the sense that patterns of gene arrangements, in such cases, are merely altered within the complement. The role of such chromosomal changes in speciation, especially in sexually reproducing plants, has been effectively demonstrated by a number of authors (26, 35, 37, 49, 59, 60, 63, 64, 66, 87, 105, 123, 153, etc.).

Nuclear changes alone cannot account for speciation. Such spontaneous changes must first undergo selection, and continuous selection results in the sorting out of well adapted mutations. Genic or environmental isolation then becomes operative, and the final result is the origin of either sympatric or allopatric species. There is no doubt that chromosomal and genic changes produce the raw materials for evolution.

The relative roles of gene mutation and alterations in chromosome structure, in the speciation in different groups of plants, can be assessed by a study of their karyotypes. The term "karyotype", by definition, implies morphological expression of somatic chromosomes; an "idiogram" is its diagrammatic representation. A comparison of the idiograms of species of the same genus or of different genera gives an indication of the evolutionary roles played by different cytological processes in addition to polyploidy.

TYPES OF CHROMOSOMAL CHANGE IN RELATION TO SPECIATION

The evolution of species in certain genera, e.g., *Quercus* (53, 130, vide 171), has been attributed principally to gene mutations. Karyotypic differences were not detected between the species of these genera with the techniques available when they were studied. A large number of new techniques have since then been evolved, and with their help, even the very minute details of chromosomes, hitherto unrecorded, have been worked out. It is desirable that these species, which supposedly contain a homogeneous karyotype, be cytologically examined again, using the refined techniques.

A number of other genera, including several of the Liliaceae (101), have also been studied, where the karyotypes of the species are nearly identical, except slight differences in detail. In *Lilium* (173), for example, the karyotypes vary mainly with respect to the morphology of nucleolar chromosomes.

On the other hand, cases are on record where every species of a genus is characterized by distinct, well defined, morphologically separable karyotypes (vide 171). The classical example of this type is *Crepis* (4), where the interrelationship between all species can be traced cytologically by a comparison of karyotypes. Extensive researches carried out on the cytotaxonomy of a number of other families and genera in recent years are yielding abundant data showing that species or other taxonomic units can be identified on the basis of their karyotypes (8-13, 31, 32, 36-39, 46, 48, 54a, 55-58, 61, 64, 65, 70, 75, 76, 79, 82a, 85-88, 88a, 93-96, 98, 102, 103, 11a & b, 115, 118, 121, 166, 167, 174, 178, 179, 181-183, 186, 194, etc). These investigations have clearly revealed how data on chromosome structure assist in determining the phylogeny and affinity of species.

Karyotypic changes can be brought about in numerous ways. It is well known that breakages, reunion in a reverse position and translocations of chromosome segments play the most significant role in this process. Speciation of plants, as affected through translocation, has been extensively reviewed by Burnham (26) on a vast number of angiospermous families, the species of which exhibit heterozygosity with respect to translocation. In addition to his list of structural hybrids, *Cipura paludosa*, a bisexual member of the Iridaceae, is characterized by a heteromorphic pair of chromosomes in its nuclei (165).

Two authors (41, 105) have fully established that centromeres do not originate *de novo*. It is therefore not likely in genera with localized centromeres that fragmentation, as it is, can account for speciation.

It is now clear that alterations in chromosome structure, through the means discussed above, have affected changes in chromosome complements in different ways. Darlington (41) reviewed the ways through which these processes can change the morphology and number of chromosomes. They are: a) reduction in chromosome number, b) change in the morphology of chromosomes, c) change in the quantity of chromatin in the entire complement.

It has been well established through study in a number of genera that reduction in chromosome number, through chromosomal alterations, has been the main evolutionary tendency in several families. In *Crepis* (4), particularly, it has been clearly shown that the primitive species contain higher basic numbers, while the advanced ones have lower numbers with altered karyotypes. Apparently, in this genus the species with different basic numbers have been derived one from the other by distinct structural alterations of the chromosome complement.

In his classical work, Levitsky (83, 84) has shown that, in the primitive tribe Helleboreae, reduction in chromosome size of the entire complement as well as of the members of the same complement has affected speciation in different degrees. He has recorded that the genus *Helleborus* contains a primitive complement, having large isobrachial chromosomes in low number. Asymmetry in the karyotype is the principal feature in the advanced genera. Similar observations have been made on *Dubyaea, Hieracium, Crepis, Youngia, Lactuca, Vicia, Lathyrus, Taraxacum* and several other members of Compositae, Helobiae, etc. (3, 4, 6, 7, 120, 131, 132, 170-172, 185, etc.). In the families Liliaceae, Amaryllidaceae, Aroideae and Agavaceae (99-101, 129), too, ample cases have been recorded where the primitive members possess the so-called "symmetrical" karyotype, the advanced ones "asymmetrical".

One of the most important manifestations of change in chromosome morphology is often detected in the morphological nature of nucleolar chromosomes. Lately, in addition to those mentioned in the classical review of Gates (59a, 50), a number of plant genera have been recorded, where the species differ mainly with respect to the morphology

of nucleolar chromosomes, supplementing other chromosomal differences (15-17, 54, 97, 112, 125, 133, 137, 145, 146, 151, 153, 167, 168, etc).

The evolutionary tendencies exhibited by nucleolar chromosomes have not yet been thoroughly studied. It cannot be stated with certainty as to which types of nucleolar constrictions should be considered as primitive or advanced. A thorough investigation is desired in this direction.

DIMINUTION IN CHROMATIN AS AN INDICATION OF STRUCTURAL CHANGES IN CHROMOSOMES

Another very significant expression of chromosomal change affecting speciation is overall reduction in size of chromosomes. Unlike translocation and inversion, this is not a process accounting for speciation directly. Instead, its expression is dependent on chromosomal changes, and it is an indication that undetectable alterations in chromosome thread, including deletion of segments, are in operation with the evolution of species. This diminution therefore is fully controlled by chromosomes. It has been argued by others that lack of phosphorus may cause such diminution in chromatin matter. This remains to be proved. In a large number of cases of polyploidy, diminution in chromatin matter is always an associated phenomenon. This becomes evident by comparison of chromosome size between most of the polyploid and diploid species. Polyploidy itself rarely results in a new character, and such diminution may be an indication that the accompanying structural changes of chromosomes, too, play a role in the expression of characters. Alterations in qualitative characters, often noticed in polyploid types, may owe their origin to such a process.

Delaunay (47) first demonstrated the gradual diminution in chromatin matter from primitive to advanced forms in the genus *Muscari*. Since then, such phylogenetic reduction in chromatin matter has been noted by a number of authors in *Crepis, Dianthus,* several members of Compositae, etc. (5, 124, 171, 185), in both annuals and perennials. It has been suggested that reduction and increase in chromosome size, as in some members of Gramineae, Polygonaceae, Cruciferae (2, 78, 92) etc., has taken place also between species of *Dianthus* (124), indicating evolution in two directions. This problem has been dealt with in detail by Stebbins (170). Recent records (155) show that in

Curculigo, a herbaceous genus, *C. orchioides* (2n=36) contains much smaller chromosomes than *C. recurvata* (2n=18). The former is a weed and can tolerate far more climatic change than the latter. *C. orchioides* is about one-tenth as large as *C. recurvata* but possesses a higher chromosome number and shows diminution in all vegetative and floral characters. It is quite likely that this reduction in chromosome size is in some way related to the diminution of all the morphological characters. Decrease in chromosome size with increase in specialization has also been recorded recently in *Chrysanthemum* (50-52).

In one of the largest tropical families, the Palmeae, cytological investigations on which have recently been made (161), the same phenomenon is predominant in most of its members. In several genera belonging to the same tribe, primitive forms contain more chromatin matter than the advanced types. Such reduction in chromatin matter in the palms is characteristic of different evolutionary series within this family. An overall reduction in all vegetative and floral characters is associated with this diminution in chromatin matter, as in *Curculigo*. In all these cases the difference in chromatin matter is so much that it cannot be attributed to the effect of fixatives. Besides, in order to eliminate such technical error, a common fixative has been used for all species.

A thorough search on this correlation is desirable in different families of plants, and such investigations are expected to yield significant data on the principle governing this phenomenon. The degree of gene change associated with this process is yet to be determined. It is not unlikely that reduction in chromosome size may be due to elimination of heterochromatic matter from the chromosomes, which obviously may result in a change in the expression of quantitative characters. The size difference is often so pronounced that it can hardly be reconciled with the idea (185) suggesting that the difference is mainly due to the degrees of coiling in the two.

At present we do not find any reason to believe that types with large chromosomes are to be found in cold climates, those with smaller ones in hotter regions, as claimed by some authors (2, 124). For example, species of *Commelina* (134, 164) with comparatively small chromosomes are found in temperate areas, while others with longer ones occur in the tropics. On the other hand, within the same genus, certain members of *Aneilema*, having longer chromosomes, have been

reported from temperate regions and others with smaller ones from the tropics. *Tradescantia* of the same family, with long chromosomes, is temperate in distribution (16, 40). From such contradictory data within the same family it appears that correlation between chromosome size and climate is not universally applicable.

Modes of speciation, so far discussed, mainly involve inversion, translocation and deletion of chromosome parts. In a majority of plants, therefore, as the literature shows, these methods of alteration in chromosome structure doubtless have played the most important role in speciation.

KARYOTYPIC CHANGES AND THE ORIGIN OF AGRICULTURAL STRAINS IN CROP PLANTS

The importance of chromosomal alteration in the evolution of crops has been demonstrated in a number of cases. Formerly it was accepted that the varieties of agricultural crops—e.g., wheat, rye, barley, sorghum —owe their origin mainly to mutations of genes. This idea arose from our former inability to detect any difference between the karyotypes of strains belonging to the same species. Recently, from studies with the aid of improved methods, it has been clearly shown that there are minute differences between the chromosome complements of different strains. In barley, for instance, some strains can be identified by their karyotypes. As no evidence of translocation heterozygosity has yet been noted in any case, it is claimed that homozygosity for translocation has been attained in them through continued cultivation and careful selection. It is suggested (136) that crossing between strains may restore the heterozygosity, thus allowing the mapping of chromosome ends, as has been done in *Oenothera* and *Datura* (14, 22, 128).

Hagberg and Tjio (67, 184) have secured petaloid x-ray mutants of barley, which differ from the normal type in translocation of a segment. Further studies have shown ring chromosomes in meiosis in this mutant—definite evidence of translocation heterozygosity. Wellhausen (191) has recently shown how the high yielding corns differ from the low yielding types in their karyotypes with respect to knob number. These are all confirmatory of the suggestion that in all probability, structural changes of chromosomes play a distinct role in the evolution of agricultural strains of crop plants.

With this change in outlook as regards the origin of agricultural strains, different genera of crop plants have been studied and more and more confirmatory evidence is gradually being accumulated. Thus, in different strains of *Sorghum* (143) karyotypic differences have been noticed, and in each strain characteristic chromosome morphology has been demonstrated. The karyotypes of strains differ mainly with respect to the number of nucleolar chromosomes in them. Breeding work in this genus, undertaken here, is gradually yielding supporting data in this aspect. Recently, in wheat, the presence of chromosomal biotypes has been worked out by some authors (2). This strain has also been found to differ from the common strain with respect to the number of nucleolar chromosomes. Recent work (24, 109, 110) on *Secale cereale,* too, is revealing that strains differ with respect to karyotypes.

FRAGMENTATION OF CHROMOSOMES AS A PHYSICAL BASIS OF SPECIATION

Fragmentation of chromosomes, too, can bring about an increase in chromosome number and thus play a distinct role in the origin of species (27-30, 89-91, 106, 107, 189). Formerly this was not recognized because it was demonstrated (vide 41, 105) that fragmentation in a normal chromosome with a localized centromere may result in fragments lacking centromeres, i.e., acentric fragments which do not survive. It has been shown, however (27, 28, 30, 189), that there are diffuse centromeres, the "polycentric" chromosomes of La Cour (82), in which a chromosome fragment can have its own centromere.

Camara and others have shown that none of the species in *Luzula* has a centromere at a localized position. The centromeric function or the property of spindle attachment is diffuse throughout the chromosome. The evidence of diffuse centromeres is borne out especially by their behaviour at the spindle. During metaphase and anaphase the two sister chromatids are arranged on the spindle, parallel to each other, and move along their entire length on the fibres. Even after critical fixation, no localised centromere could be brought out in them.

The chromosome number of most species of *Luzula* is a multiple of six. The most primitive, *L. purpurea,* has $2n = 6$, while the other species contain 12, 24, 48, 96 and more chromosomes. The higher the chromosome number, the more advanced is the species. In other

words, evolution here is associated with multiplication of chromosome number.

It is significant that this increase in chromosomic number does not involve polyploidy. The most primitive species with the lowest chromosome number, $2n = 6$, is characterized by the largest chromosomes in the genus. With progressive multiplication, there is gradual reduction in chromosome size. This is so marked that the chromosome size of the species with $2n = 12$ is half that of the $2n = 6$ chromosome species. This implies that the chromatin matter in all species is the same, though the chromosome number in each of them is different.

On the basis of these facts, it has been assumed that evolution within this genus has involved fragmentation of chromosomes at different loci and subsequent behaviour of the fragments as independent chromosomes. The diffuse nature of the centromere facilitates survival of the fragments, as the latter, having diffuse centromeric property, can attach themselves to the spindle. This provides them with a method of increasing chromosome number other than polyploidy. Meiotic data obtained from hybrids (106, 107) support this assumption. In crosses involving one species with low and another with high chromosome numbers, such as *L. purpurea* ($2n = 6$) and species with $2n = 12$, each chromosome of the former, pairs, in its different segments, with two chromosomes of the latter. This is to be expected if the small chromosomes of the species with higher number are considered as products of fragmentation of longer chromosomes of the species with low number. Irradiation with X-rays has caused fragmentation of chromosomes, and subsequent behaviour of the fragments as independent chromosomes has furnished definite evidence in support of this (29).

The findings of Camara and his school have opened up a new evolutionary aspect, that is, fragmentation of chromosomes as a physical basis of speciation. It has been claimed that diffuse centromeres indicate primitiveness; they have been noted in *Carex, Scirpus, Juncus* and other genera (68, 69, 71, 175, to 177, 190, 193). Vaarama (188), too, assumes that the diffuse type of centromere represents a primitive state, the localized type—an advanced stage. In some algae, too, such diffuse centromeres have been noted (62), suggesting that a thorough search with the aid of adequate methods may reveal its presence also

in other groups of plants. La Cour (82) regards the chromosomes of *Luzula* with diffuse centromeres as of polycentric nature, a term often applied to certain animal chromosomes. This controversy is one of terminology. To assume that a polycentric chromosome arises by innumerable translocations would involve too much speculation, amounting to absurdity.

Bhaduri and Bose (18) interpreted certain interesting data obtained in species of Cucurbitaceae by assuming fragmentation of chromosomes as a physical basis of speciation. They suggested that fragmentation across the loci of the secondary constriction regions is responsible for the increase in chromosome number in some genera, e.g., *Cucumis*, of this family. This theory has been further elaborated in species of Musaceae by Chakrovorty (33, 34). Most of the species of *Musa* are characterized by normal monocentric chromosomes with supernumerary nucleolar secondary constrictions. Some chromosomes bear even four or five secondary constrictions. Thus, often the total number of secondary constrictions exceeds the number of chromosomes in a complement. In the primitive subgenus Physocaulis, which is represented by species like *Musa superba* ($2n = 18$), the number of secondary constrictions is higher than that in the Eumusa section, e.g., *M. acuminata* ($2n = 22$). It has been claimed that the greater chromosome number in the latter species has been brought about through fragmentation across the loci of supernumerary secondary constrictions in certain chromosomes of the former. Karyotypes of varieties representing intermediate stages in such a derivation have also been worked out. As many as 34 secondary constrictions have been noted in *M. paradisiaca* sub-sp. *sapientum*, having $2n = 22$ chromosomes. Detection of 34 nucleoli, following Feulgen-Light Green staining of the telophase nuclei of somatic cells, shows that all these secondary constrictions are nucleolar.

These observations raise a different problem, that is, whether a centromere can originate de novo. If the interpretation of the abovementioned authors is correct, it must be assumed that a centromere can originate de novo, which, as far as evidence shows, is quite improbable. Therefore, though this idea of fragmentation provides a reasonable basis of increase in chromosome number without polyploidy, it remains to be proved by experimental evidence.

In the light of observations on *Luzula* and the theory advanced by

Camara, a modified interpretation of data on *Musa, Cucumis,* etc. can be presented. It is quite likely that fragmentation of chromosomes, as suggested by workers on Cucurbitaceae, Musaceae, etc., is responsible for speciation within these genera. But their interpretation regarding the means by which this process has been operative involves the assumption that a centromere can arise de novo—a suggestion so far remaining unproved. A reasonable solution of the problem is to assume that fragmentation must have occurred quite early in evolution, at a stage when the ancestral forms of these species might have possessed diffuse centromeres. Later, during the course of evolution, such fragments with diffuse centromeres had the centromeric function localized at a particular segment of the chromosome, as we see them now. Since fragments with diffuse centromeres can behave as normal chromosomes, as noted in *Luzula,* this interpretation does not necessitate the centromere originating anew. However, this theory presupposes that the ancestral forms of *Musa* possessed diffuse centromeres, which has not yet been proved. But, even then, considering the existence of diffuse centromeres in certain groups of plants and the absolute improbability of a centromere originating anew, the interpretation presented here seems to be the only means by which fragmentation of chromosomes can be assumed to have affected speciation in this genus. A thorough study of the primitive and wild species of *Musa* may support this assumption. Even though primitive species of *Musa* with diffuse centromeres are not found, this interpretation does not become invalid in any way. It is possible that the long period of evolution which has resulted in specialization of the different species of *Musa* in a number of features, may have gradually led also to the extinction of the highly primitive forms, being not fitted to survive in competition with better equipped ones.

A TENTATIVE SUGGESTION REGARDING THE EVOLUTION OF CHROMOSOME STRUCTURE

The reality of the diffuse centromere may be accepted as established by available data. This finding may be regarded as filling a big lacuna in our knowledge of evolution and speciation in general.

On the basis of all these data, the sequences of evolution may be outlined as follows:—

a) In certain algae, e.g., Myxophyceae, no definite nuclei are present.

The corresponding structure in the blue-green algae is known as the "central body". It does not contain any chromosome, but appears to have desoxyribonucleic acid and, in all probability, particles of desoxyribonucleoprotein. It may represent an early step in evolution, where gene particles in the DNA-protein are diffused throughout the cytoplasmic mass. Localization of function in distinct genes linearly arranged in special bodies, the chromosomes, a character attained by other groups of plants, is lacking in them. The possibility of the genes being in a diffuse state is indicated by the claim of cytoplasmic genes in a number of plants and animals.

b) The presence of diffuse centromeres in algae as well as in primitive higher plants suggests that in the latter the centromere function has not been localized, although localization of another function has been attained to the extent that genes are arranged in discrete bodies, the chromosomes. It is therefore a step much higher in the series of evolution than that represented by the possession of a central body.

c) A still higher step in evolution is possibly represented by plants possessing localized centromeres and a large number of constriction regions or unstained gaps in their chromosomes, e.g., *Musa, Trillium* and *Fritillaria* (33, 34, 42, 43, 126). Four and five such supernumerary constrictions in each chromosome have been found in a number of primitive species of *Musa.* All of them are directly concerned with a common function—nucleolus organization. In the other two genera there are several heterochromatic regions, the so-called "nucleic acid-starved" areas of Darlington (42), which may or may not be nucleolar. This issue is yet to be worked out. In any case, their heterochromatic nature suggests that, as in *Musa,* these constrictions, too, perform a general and common function, that is, the function of heterochromatin but not production of nucleoli. It is therefore implied that in these cases, a common function is performed by a number of chromosome segments, or, more precisely, that no single specialized region is set apart for performing a particular function, for example, the production of nucleoli in *Musa.* In other words, distinct localization of this function has not yet been attained by the chromosomes of such plants. As the centromeres in these species are localized, they represent a step higher than those showing diffuse centromeres but lower than these where organization of the nucleolus, too, is much more localized in the chromosomes than in *Musa* or where the heterochromatin function

is carried out by one segment or a lesser number than in *Trillium, Fritillaria,* etc.

d) The final step, the culmination of the series, which may be assumed at the present state of our knowledge, is represented by the majority of higher plants, where the chromosomes possess a single centromere and the nucleolar chromosome is provided, in addition, with a single secondary constriction. The detactable heterochromatic segments are few.

The above genera, according to taxonomists, do not represent steps in a single line of evolution but may be considered as indicating steps in evolution which have run parallel in different groups, the general sequence of chromosome development being the same in all.

We are fully aware of the limitations of the data forming the basis of the above thesis. It is suggested that, in view of the evidence at present available, this may be treated as a hypothesis, the validity of which is yet to be tested by a large number of observations on different species, both primitive and advanced, representing all major groups of the plant kingdom.

INCONSTANCY IN CHROMOSOME COMPLEMENTS WITHIN A TISSUE AND ITS SIGNIFICANCE IN SPECIATION

Speciation, as it is effected through the different means outlined above, has been discussed except in certain species of *Musa* which reproduce by sexual means. In all cases discussed above, therefore, such alterations, whenever occurring, must be present in the germ cells to become effective in the origin of species. Certain cases are known where apomixis has helped in the diversification of forms (104, 111, and vide 171). Somatic mutations in most cases if at all they occur, are obviously gradually eliminated. No doubt, cases of occasional bud mutations are also known, but they too are maintained later through sexual reproduction.

What, then, has been the means of speciation in the vast majority of monocotyledonous plants, where sexual reproduction is obsolete and propagation is principally, in some cases entirely, vegetative. Most bulbous plants used in horticulture belong to this group. In a number of these plants, such as several tropical aroids, flowers are scarce. They are cultivated because of their specialized leaves. In other cases, though flowers are formed regularly, seed-setting is never observed, for example,

Hemerocallis and *Polyanthus* (101, 155). In some of them effective P.M.C.'s are not formed. In others, if formed, P.M.C.'s show irregularities; and in still others, though meiosis appears to be normal, there is a high degree of pollen sterility and irregularity in megaspore formation. These factors are evidently responsible for lack of seed-setting.

None of these genera can be considered as representing a static step in evolution, as most of them possess a large number of species. They are dynamic and successful genera, producing variable new variants, both in nature and under cultivation. The problem arises as to the nature of their present means of speciation. As sexual reproduction is obsolete in them, the chromosomal alterations produced do not go into the formation of gametes. Therefore speciation in these cases obviously is effected through vegetative reproduction.

An interesting phenomenon was recorded in *Caladium bicolor* (149), a member of the Aroideae, cultivated for its ornamental leaves. The species includes a number of varieties characterized by $2n = 28$ chromosomes. In the somatic tissue of these varieties the chromosome complement is not fixed but varies in structure and/or number in different cells of the same tissue. The number in the highest frequency is considered as representing the 2n complement. There is considerable meiotic irregularity and seed setting is absent. No distinct zonation of these variations could be worked out, for they occur at random.

A cytological study of the different varieties and allied species revealed that all of them are characterized by distinct karyotypes, though showing the same number. A significant feature is that an abnormal complement of one variety becomes the normal complement of another variety. It has, therefore, been inferred that, as sexual reproduction is ineffective, such constant alterations in the somatic tissue play a distinct role in speciation, the process being effected through vegetative reproduction. This provides them with an effective means of speciation without dependence on complicated sexual reproduction.

It is noteworthy that in a few plants, variations in chromosome complements in the somatic tissue were reported by some workers previously and have been even very recently (1, 19, 25, 80, 119, 127, 187), including the present writer in his earlier works. The significance of such variations could not be worked out then and so were mainly referred to as abnormalities. No significance from the point of view of speciation could be assumed. This outlook was due to the bias

that sexual reproduction is the only medium through which speciation operates.

With the realization of the importance of this phenomenon in speciation from work on *Caladium bicolor* (149), investigation was extended to many vegetatively propagating plants, especially to the families Liliaceae, Amaryllidaceae, Aroideae and Dioscoreacae. Improved methods have been followed so that a high frequency of division and clarification of karyotypes, with the maximum possible details, could be obtained. Publications from time to time, outlining the results of these investigations, have distinctly proved the regular presence of such variations in the somatic tissue of all species so far investigated (21, 99-101, 135, 137-139, 141, 144, 152, 154-157, 159, 163). Definite evidence has been obtained from karyotype studies of the possible origin of one variety from another. More than 200 species have been examined and reported, and all of them show the same behaviour.

An instance (101) may be cited of the derivation of one variety from another. In *Hemerocallis manorama,* a horticultural type, there are two varieties, one with 24, the other with 22 chromosomes (101). The latter shows 24 chromosomes in its abnormal nuclei. It is quite likely that one type ($2n = 24$) owes its origin to the other ($2n = 22$) through vegetative reproduction as altered nuclei with $2n = 24$ chromosomes entered the growing tip of daughter shoots. This is the only way this variety could have originated, since sexual reproduction is obsolete in this species.

Discrepancies in reports of chromosome numbers of the same species as well as of different chromosome numbers in different individuals of the same species (vide 13b, 13c, 45, 129, 135) can also be explained on the basis of this theory. To cite a few instances, 2n in *Eucharis grandiflora* has been given as 44 and 68 (99, 129), in *Hippeastrum rutilum* as 44 and 49, and in *Hymenocallis calathina* as 74 and 60 (99, 129). Kurabayashi and Samijima (81) have recently reported variation in structure of chromosomes in different populations of *Paris tetraphylla.* Similarly in *Polygonatum verticillatum* Thernan has reported (181) chromosomal biotypes within a single species. Such cases are well known in *Saccharum* (112), too. It is likely that in all these vegetatively reproducing plants, chromosomal biotypes have arisen through asexual propagation. Different chromosomal biotypes have obviously been studied at different times by different

workers, and so discrepancies are noted in their reports. Such biotypes differ from one another either in number or in structure of chromosomes. On the basis of such evidence, it has been postulated that in plants where vegetative reproduction is nearly or completely obligatory, speciation is effected through the entrance of nuclei with altered karyotypes into the growing tip of daughter shoots, thus forming new shoots in the course of propagation.

Recent investigations in this laboratory show that this behaviour and consequently this means of speciation are the rule in those dicotyledonous plants, too, that are propagated mainly through cuttings or graftings, e.g., *Bougainvillea* (148, and unpublished observations by Sharma and Bhattacharyya). In a large number of pteridophytes (156, 157) the same phenomenon seems to be operative, acting through apogamy and vegetative reproduction.

The same evolutionary process may be operative in a large number of dicotyledonous species, reproducing both sexually and asexually where different chromosome numbers have been reported in the same species. Variation in chromosome number in the somatic tissue of a number of dicotyledonous genera, e.g., *Mentha* and *Piper*, have already been obtained (147). All of them reveal widely different 2n numbers in different individuals of the same species, for example, 2n = 36, 64, 66, 68 and 70 in *Mentha piperita* (vide 45, 147). It can be argued that biotypes can arise here through sexual means which is quite effective in them. But in view of the fact that meiosis in them seems normal, it appears that such variant nuclei do not participate in the formation of gametes. Even if they could participate, nonviability of the gametes may be one of the possible consequences in view of such wide variation of number. In consideration of this fact and also because of the inconstancy in chromosome numbers already noted in the somatic tissue of a number of dicotyledonous species, it is suggested that speciation is effected here not only through sexual but also through vegetative reproduction. Extensive critical investigations on the chromosome complements of somatic and meiotic tissues of dicotyledonous species having a number of chromosomal biotypes are extremely necessary to work out the relative role of sexual and asexual means in their speciation.

Investigations are now being carried out on the mode of origin of such variations. Regarding the origin of structural variations, ample

evidence of breakage and translocation of chromosome segments in these plants has been brought forward, and different karyotypes have been traced, one from the other, assuming the operation of such processes (135). As to numerical variations, somatic reduction and to some extent non-disjunction have been found on a large scale within these tissues.

Somatic reduction was first demonstrated with sodium nucleate, low temperature and other methods (72-74, 113, 114, 192). A number of publications on somatic reduction have since shown that disturbance in the nucleic acid balance can cause reductional separation of chromosomes in somatic tissue (140, 142, 150, 158, 162); also that cells with different chromosome numbers can arise out of somatic reduction, as the process does not necessarily involve half-and-half separation to the two poles.

The regular occurrence of somatic reduction in plants reproducing asexually indicates that this process is possibly responsible for the origin of varying chromosome numbers. As reductional separation is caused by nucleic acid disbalance, it is not unlikely that the cells which do not maintain a proper ratio of nucleic acid, provide for its occurrence. Abnormalities in chromosome number and consequent variation in nucleocytoplasmic ratio suggest this. Once an irregularity has arisen through an upset of nucleic acid balance, it can easily be relayed by successive divisions throughout the tissue. The exact factor responsible for initiation of irregularity and disturbance of nucleic acid balance is yet to be explored. As this behaviour is characteristic of all asexually reproducing species so far studied, gene mutation may be considered responsible for its origin, the mutant being well fitted for vegetative reproduction.

Various problems obviously arise in view of this apparently irregular behaviour and speciation while propagating through vegetative means. These are:

a) In a number of genera, e.g., *Hemerocallis* and *Hymenocallis*, the species differ chiefly in chromosome structure and not in number. Why?

b) Why are sterile flowers regularly produced in some species but are scarcely noted in others?

c) How is the nucleo-cytoplasmic balance maintained in tissue which contains varying chromosome complements?

A majority of these species differ only in their karyotypes. This

implies that variations involving structural alterations of chromosomes have aided in the origin of species through their participation in daughter shoots. This is quite likely in view of the fact that, of structural and numerical variations, the former are better fitted than the latter for competition because of their normal number. The greater the difference from the normal, the lesser is the chance of survival. However, these numerical variations may sometimes survive, the result of which is the origin of individuals with altered chromosome numbers, as noted in some species.

As regards the second problem, that of regular and rare occurrence of flowers in this category of plants, it seems likely that this is the result of human interference and selection. All the species of *Hemerocallis, Pancratium, Amaryllis,* etc. are cultivated by horticulturists mainly for their showy flowers. Naturally, somatic mutations which do not possess the capacity of flowering regularly are not favoured and are eliminated in selection by horticulturists .All preserved variants have retained the capacity of blooming. The reverse prevails in aroids, where species which seldom flower are mainly cultivated for their foliage.

Lastly, with regard to the problem of nucleo-cytoplasmic balance, some insight can be gained if the mode of origin of such variations is taken into account. Nucleo-cytoplasmic balance is possibly maintained here in a different way than in sexually reproducing plants. This balance cannot be identical for all cells, as different complements are present in the same tissue. Since all these variations arise out of breakages, translocations, non-disjunction and somatic reduction, they result in a different arrangement of chromosome segments and chromosome number in the variant nuclei, without addition of chromatin as in polyploidy. Due to this mere reshuffling of the complement, the nuclear and cytoplasmic matter in the tissue, as a whole, remains possibly nearly the same, though that in the individual cells may vary. It is quite likely, therefore, that the nucleo-cytoplasmic balance in this specialized group of plants is maintained, not in the individual cells but in the tissue as a whole. Therman (180), who noted inconstancy in tumour brain cells, came to the same conclusion regarding nucleo-cytoplasmic balance. Chemical analysis of nuclei and cytoplasm with the aid of isolation technique may prove to be of help in solving this problem.

So far as animal cells are concerned, there are numerous cases of

such aneuploid inconstancy (25a, 127, a, b; 180; 190a), though contradictory observations, too, have been recorded (13a). At present it is not possible to state precisely how far such inconstant behaviour is significant in the life of an animal.

CONCLUSION

The above resumé is a clear indication of the tremendous advances in chromosome studies within the last few years. This is mainly due to the continued realization of the necessity of a critical study of chromosome structure in solving several debated problems of phylogeny and evolution. It has been fully established that the study of chromosome structure is a specialized science in itself, requiring contributions from cytology, genetics, biochemistry and biophysics for solution of its problems. Whatever advancements have been made are due to the co-operative efforts of different groups of workers.

A glance at the progress attained, which is outlined in the preceding article in this journal (Oct.-Dec., 1958), reveals enhancement of our knowledge regarding the fundamental nature of chromosomes, both physical and chemical, and the exploration of a number of important aspects of their behaviour and their significance in speciation.

Recent advancements regarding the physical and chemical nature of chromosomes have distinctly proved that the fibrillar structure is a reality. It is also settled that the number of microfibrils is not less than 32. The structure of the centromere, which was considered till recently to be a controversial issue, has been fully clarified and its quadruple spherular nature is now well known. In addition to different types of centromeres studied, there is evidence of a new type of diffuse centromere in plants. Though the nature of secondary constrictions has not been fully clarified, they have at least been proved to be specialized segments in chromosomes, set apart for nucleolar production and not merely representing a phase in the allocyclic nature of heterochromatic segments.

The progress in our knowledge of the chemical nature of chromosomes has practically outrun that attained in all other aspects of chromosome studies within the last few years. Refinements of isolation and in situ techniques are mainly responsible for this progress. Through recent researches it has been established that not only a simple protein and DNA constitute the chromosome structure, but that other con-

stituents, such as RNA and non-basic protein, too, contribute to their formation. The structure of euchromatin and heterochromatin has also been clarified to a great extent. It has been definitely proved that plant and animal chromosomes differ in a number of fundamentals, and their separate studies have been emphasized. The improved techniques have helped these studies to a great extent.

In the light of these developments, the gene concept, too, has undergone much revision, and further complexities or structure have been reasonably claimed. Its compound nucleoprotein nature appears to be established, and evidence indicates that its specificity depends on both nucleic acid and protein components. With the refined techniques now at hand, it may be confidently expected that in the near future, more insight into the structure and the principle controlling the specificity of this hereditary material will be obtained.

In chromosome study in relation to speciation, advancement of an outstanding nature has been made. The importance of structural alterations in the origin of agricultural strains, hitherto unsuspected, has been clearly brought out. A new avenue of research has been opened up, constituting chromosomal studies in strains of agricultural crops with the aid of critical methods. Such studies have great potentialities. Cross-breeding experiments between strains having karyotypic differences are yielding good materials for mapping chromosome ends in crop plants.

A number of plant species, studied within the last six or seven years, are revealing structural differences between the chromosomes of allied members. This not only emphasizes the fact that alterations in chromosome number play a far greater role in speciation than was envisaged before, but at the same time also reveals the importance of karyotype study in the identification of a species.

The discovery of an entirely new means of speciation, namely fragmentation of chromosomes, is no less remarkable than the other discoveries. Revelation of this phenomenon has not only given a better understanding of the intricacies of the speciation mechanism in plants, but also has filled important lacunae in our knowledge of evolutionary processes.

The idea regarding the origin of species in plants, where sexual reproduction is obsolete, had long remained in a nebulous state and almost nothing was known about it. The discovery in recent years of

the inconstancy of somatic chromosome complements in this category of plants, is utterly contrary to the original concept of fixity of chromosome number in plants. The importance of such behaviour in speciation, worked out lately in detail, can be regarded as having filled a major gap in our knowledge regarding the fundamentals of speciation. The implications of such behaviour in speciation seem to be more far reaching than originally thought. This is due to the fact that recent investigations are gradually revealing that a number of dicotyledonous species whose individuals differ widely in chromosome number from one another, show similar behaviour.

All these achievements in different aspects of chromosome study have opened numerous fresh avenues of research. They mainly serve as indications of different unexplored paths, providing fresh approach to the problem of chromosome studies. Technical background, though not free from limitation, has already been prepared and has paved the way for refinements in methods and far-reaching results of future investigations.

FURTHER RESEARCH

The purpose of this review would not be fully served if some of the important fundamental issues which emerge from the above resumé are not pointed out, as they need clarification.

Apart from those aspects, such as the nature of chromosome fibrils and of genes, on which vigorous researches are in progress, some other fundamental problems still remain unexplored. For instance, the exact chemical constitution of constrictions, which are nucleolar, remains practically unknown. With the invention of recent cytochemical methods, new possibilities have been opened up towards complete chemical analysis of these regions, whose clarification is essential for gaining insight into the ultimate structure of chromosomes. Further, these constrictions differ in their morphology from each other. The evolutionary significance of this is yet a problem. A critical study involving clarification of karyotypes in primitive and advanced groups of plants is expected to yield data in this direction.

Another important issue requiring elucidation is the nature of the centromere in a number of families of angiosperms. The figures of chromosomes so far presented in the cytological literature relating to a number of grasses, rushes, aroids, etc. give no indication of their morphology. They simply appear as swollen specks or minute rod-like

structures within the cell. A detailed study of their morphology with the aid of the latest techniques and of their behaviour in anaphase is very much desired. Such studies are expected to reveal whether they possess localized constriction or whether the centromere in them is of a diffuse nature. It is not unlikely that certain plants may be found to possess diffuse centromere, a situation which, being an indication of primitiveness, will throw considerable light on their phylogeny and interrelationships with allied genera.

Another issue, still remaining uninvestigated, is the problem of nucleocytoplasmic balance in the somatic tissues of plants which reproduce entirely through vegetative means. As varying chromosome complements have been found in the same somatic tissue, it has been suggested that this balance is maintained not between the nucleus and cytoplasm of individual cells, but within tissues as a whole. A thorough chemical analysis of nuclear and cytoplasmic matter is highly desired with the aid of isolation techniques to find out whether any such constancy is maintained in all individuals of the same species.

Irregularities in the somatic tissue of this category of plants have been attributed chiefly to breakages, translocation and reductional separation of chromosomes. It has further been worked out that, so far as the last process is concerned, nucleic acid disbalance in the cell is responsible for its occurrence. The cause of such nucleic acid balance, which seems to occur regularly in every individual, is not yet known. The controlling factor of this process, which may be due to specific gene mutations, also has not been determined.

In a number of plant species, considerable diminution in chromatin matter has been noted to accompany evolution. Its evolutionary significance has been pointed out. The exact manner through which this diminution is brought about is not yet thoroughly known. The meagre data available on this aspect are negligible. It is likely that this diminution involves principally gradual elimination of heterochromatic matter from the cell. If this is proved, it will make the study of heterochromatin essential in tracing the phylogeny of plants.

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